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 GROUPS OF ALOUATTA PALLIATA PIGRA LAWRENCE 1933
 IN NATURAL ENVIRONMENTS IN BELIZE AND GUATEMALA.

DEGREE FOR WHICH THESIS WAS PRESENTED MASTER OF ARTS

YEAR THIS DEGREE GRANTED 1980

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PARENTAL BEHAVIOR - A SOCIALIZATION PROCESS
IN GROUPS OF ALOUATTA PALLIATA PIGRA LAWRENCE 1933
IN NATURAL ENVIRONMENTS IN BELIZE AND GUATEMALA



BY
INGE BOLIN

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF ARTS

DEPARTMENT OF ANTHROPOLOGY

EDMONTON, ALBERTA

FALL, 1980

80-71

THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled PARENTAL BEHAVIOR - A SOCIALIZATION PROCESS IN GROUPS OF ALOUATTA PALLIATA PIGRA IN NATURAL ENVIRONMENTS IN BELIZE AND GUATEMALA submitted by Inge Bolin in partial fulfilment of the requirements for the degree of Master of Arts.

TO MY PARENTS

ABSTRACT

Parental behavior in Alouatta palliata pigra was observed in the region of Bermudian Landing / Belize and in Tikal / Guatemala from December 1978 to March 1979, with the purpose of relating parental behavior to the prevailing monogamous group structure. Low visibility in Tikal allowed only spotty observations on three groups of howlers with two infants. In Belize visibility was excellent and observations were made on six groups of howler monkeys containing nine infants. The data were analyzed at three levels of generality.

For each infant an individual behavioral profile was established relating the frequency and duration of its social and non-social interactions. Patterns of social interactions were compiled, giving frequency, duration, and type of interactions between an infant and its respective group members. Great variability was detected among parental behavior patterns within the six groups.

At the next level, infants were categorized into three age classes to examine change in the patterns of parental behavior in the course of a howler's infancy. The results indicated a steady trend away from the mother in favor of interactions with the physical environment while, with one exception, interactions with group members other than the mother remained virtually static regardless of age. Male parental behavior was expressed more with increasing age of the infant. A light trend toward peripheralization was apparent in the older infant.

Finally, an average, derived from the patterns of interactions of all nine howler infants, was used in a general comparison of parental behavior in Alouatta palliata pigra with that of other monogamous

species and with polygynous and polygamous species of Alouatta as reported in the literature. It became evident that although the mother was the prime caretaker, the male did participate more actively in the raising of the offspring than is known from polygynous and polygamous groups of howlers. Infants were responsible for most of the initiations and terminations of interactions.

Great permissiveness on the part of the parents and their attempts to promote early independence in the infants were strong trends detected in the parental behavior patterns of Alouatta palliata pigra. Within the disturbed environment in Belize, these trends would be adaptive.

ACKNOWLEDGEMENTS

It is impossible to individually acknowledge all the people who have contributed to the completion of this project.

I wish to thank my supervisor, Dr. Linda Fedigan, her husband Dr. Laurence Fedigan, and the members of my thesis committee, Dr. Ruth Gruhn, and Dr. Jan Murie for their assistance, encouragement and constructive advice throughout the writing stage of this thesis.

My very special gratitude goes to Dr. Melvin Neville who assisted me throughout the project with enthusiasm and whose expertise on Alouatta and long field experience were invaluable to this study. Drs. John and Janice Baldwin and other investigators of primate behavior as well as Dr. Faust, Dr. Kirchshofer and Dr. Jantschke of the Frankfurt Zoo in Germany deserve my deepest thanks.

I am much indebted to many friends and colleagues in Peru, especially Dr. Antonio Brack, Ing. Ramon Ruiz, Rogerio and Meri Castro, Maria Coppula, Pekka Soini, Renan and Gabriela Loja, Juan Tapullima, Abertana Paima, and Juanita and Gunter Schaper, who introduced me to fieldwork in primate behavior and who made me feel at home in the jungles of the Upper Amazon.

Many wonderful people in Belize and Guatemala assisted me during my fieldwork, among them Dr. Luis Lujan, Dr. Rudy Larios, Richard Foster, Hubert Baptist and Rudolph Joseph.

Most of all I want to thank my husband and children, without whose love, dedication, and support this study would not have been possible.

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CHAPTER ONE

INTRODUCTION

Among non-human primates we find a great variety of parental behavior patterns ranging from minimal parental care, as exhibited by the tree shrew (Tupaia glis), to intensive care that lasts for many years, as seen in the great apes. The diversity of patterns involves not only the intensity of care and the time span of the dependency of an infant, but also the degree to which different members of a group administer parental care. Thus, for example, in feral orang utans (Pongo), the mother exclusively cares for her offspring, while in monogamous species of New World Primates, such as the pygmy marmoset (Cebuella pygmaea) or the night monkey (Aotus trivirgatus), the father participates greatly in the care of the offspring. In other species such as Japanese macaques (Macaca fuscata) and hamadryas baboons (Papio hamadryas), 'aunts', siblings, and males share in parental care.

The extent to which parental caretaking patterns are genetically determined, or are a function of the environment or of socialization processes within groups or species, remains to be determined. Although I believe that all these factors can be instrumental in shaping parental caretaking patterns, this investigation of the behavior of free-ranging Alouatta palliata pigra deals primarily with socialization processes.

Studies concerning effects of group structure and socialization on infant development have a considerable history. As early as 1934, Carpenter proposed that an investigation of simian social relations and behavior requires an analysis of the way in which animals of a particular family, genus, or species are organized. He deemed it

desirable to determine the number and kind of animals which compose the groups, as well as the central tendencies of these groupings.

Altmann (1959) stressed the importance of behavioral studies in primates relating to early infancy, a period when intraspecific differences in behavior are determined. Poirier (1977:17) echoes the above authors' views, suggesting that "group structure reflects and influences individual behavior; not only the form of group organization, but group life itself, is dependent upon the early environment of individual animals". Baldwin and Baldwin (1973) and Neville (1972a) also emphasize the study of ontogeny within groups that are structured differently.

In an attempt to relate group structure to parental caretaking patterns, Redican (1976) devised the following general hypothesis based on a variety of studies: in monogamous family units - composed of an adult male and female mated primarily for life, together with their offspring and only occasionally one or two other adults - the male participates to a great extent in the raising of the young. In polygynous groups the male is involved in parental care, although to a lesser degree than in monogamous groups, while in polygamous groups, the mother alone often cares for the offspring. Although with regard to polygynous and polygamous groups this generalized rule is not consistent in all species, considerable male participation in raising the offspring is a fairly consistent pattern in monogamous groups.

The genus Alouatta lends itself well to a study of parental behavior in relation to group structure, since within this genus and even within the same species - Alouatta palliata (mantled howler) and Alouatta seniculus (red howler) - we find all three major grouping patterns: monogamous, polygynous, and polygamous. However, throughout

most of the published reports (Carpenter, 1934; Altmann, 1959; and others), Alouatta is referred to as a polygamous species with occasional polygynous groups.

The poor survival record for Alouatta in captivity has not allowed for significant research. Of the few observations on monogamous groups of Alouatta in the wild, none related to parental behavior.

The present research on parental behavior in Alouatta palliata pigra is concerned with the relationship between group structure and parental behavior patterns. Parental behavior, as it existed in six groups that I studied in Belize, is analyzed in light of the prevailing monogamous grouping pattern. The central question focuses on the issue: how does parental behavior in monogamous groups of Alouatta palliata pigra compare with parental behavior in monogamous species elsewhere and with polygynous and polygamous groups of Alouatta? Further important issues of this study relate to the adaptive value of parental behavior in Alouatta palliata pigra.

Parental behavior has no broadly established definition in the literature (Mitchell, 1977; Mitchell & Brandt, 1972; Breuggeman, 1973; Rosenblatt, in Hinde & Simpson, 1975). I define Parental Behavior as any behavior solicited by infants and/or administered to infants by the mother and the adult male, which in the monogamous groups of Alouatta palliata pigra are known to be the parents. In order to analyze parental behavior correctly, it is important to record all interactions that occur between the infant and other group members, as well as the infant's non-social interactions, since they may reflect aspects of parental behavior. For example, a small infant's rough play with an older peer or its extended excursions into the environment are reflective of a

permissive parent. Thus, a description of the full range of an infant's social and non-social interactions reveals the whole spectrum of parental attitudes.

Parental behavior as manifest in six groups of Alouatta palliata pigra is discussed at three levels: 1. the individual, 2. the age class, 3. the species.

1. The Individual

Hinde (1978) suggests that differences in group structure are consequences of differences in the social behavior of individuals. He further remarks (1974:229) "as soon as one starts to observe early social development, one is struck by the extent of the differences among individuals". Mason (1976:450) proposes that "the unusual and distinctive features in the evolution of primate social life are to be found in the social processes and social dynamics that produce it: and these depend ultimately on the psychological characteristics of the individual".

All individuals in the six groups - except for two older female juveniles in group IV and two adult males in group I - could be recognized individually, a fact which made it possible to establish, for each of the nine infants, an individual behavioral profile consisting of social and non-social patterns of interactions. Emphasis in this section is placed on the individual variability among infants.

2. The Age Class

At this level parental behavior is examined with regard to changes that took place at different stages of an infant's growth. Mason (1973a) suggests that an infant must perform two major developmental tasks at different points in its life cycle: the first is to maintain contact with the mother; the second is to prepare itself to

function as an adult. Three different age classes were established in accordance with Carpenter (1965) in the attempt to trace changes in parental behavior with age of infants in Belize.

3. The Species

Certain species-specific behaviors are ascribed to every animal species, despite the fact that generally we find variance between groups as well as among individuals of the same group or the same age-sex class. Parental behavior patterns as they emerged in the six groups are useful in describing average tendencies of parental behavior in Alouatta palliata pigra, as well as an interpretation of the effect of parental care on the social order for the species. The findings are used in a general comparison with other species of Alouatta and with other monogamous species.

In addition to the above, howler characteristics widely described in the literature, such as permissiveness toward infants by the respective group members, intra-group tolerance, great adaptability to different ecological niches and considerable flexibility in grouping behavior, are discussed in reference to the study groups.

CHAPTER TWO

REVIEW OF THE LITERATURE

1. Related Studies on Parental Behavior in non-human Primates

Mother-infant relationship.

Many socialization studies have focussed on the mother-infant relationship which is held by primatologists to be the earliest, the strongest, and the longest social bond (Poirier, 1977). The strength and intensity of this mother-infant bond, which is essential for adjustment of the offspring to intra- and inter-group relationships as well as for establishing an intense learning situation, has been demonstrated by a variety of studies in the wild and in the laboratory (Harlow, 1963; Jensen et al., 1967a; Jolly, 1966; Poirier, 1968, 1970, 1972, 1973; and others). Physiological and morphological states influence the nature and extent of the early dyad, but psychological states and social habits formed during infancy influence the nature and extent of social relationships which persevere later in life (Tinklepaugh, 1948).

Some of the best studied variables which affect the mother-offspring bond as well as the later life of the offspring are the mother's parity, her rank or status, the way in which she treats her male versus female infants, and the permissiveness with which she allows her infant to interact with other group members. Of these variables, only 'permissiveness' is relevant to the present study. The mothers' parity was unknown in the feral howlers of Belize, rank or status is weakly developed or non-existent in howlers, and the ratio of seven male to two female infants did not allow for a quantitative analysis of maternal treatment.

The effect of the mother's permissiveness upon the bond she develops with her offspring as well as upon the relationship between the infant and other group members has been observed in two different species of langurs (Presbytis) (Jay, 1965), in Nilgiri langurs (Presbytis johnii) (Poirier, 1968), South Indian langurs (Presbytis entellus) (Sugiyama, 1967), in bonnet macaques (Macaca radiata) and pigtail macaques (Macaca nemestrina) (Rosenblum and Kaufman, 1967).

Male-infant relationship.

Unfortunately male-offspring interactions have not been well documented for any species of non-human primates. Redican (1976) suggests that the reason for the relative neglect of male-infant interactions in non-human primates is due to the fact that species exhibiting the greatest amount of paternal (male) care are forest dwellers, the study of which is considerably more difficult than that of terrestrial primates. The scarcity of studies should not, however, deflect from the potentially great importance of male parental behavior patterns upon the behavioral development of the infant, even in groups where the male does not take a predominant role in the raising of the offspring.

As pointed out earlier, male participation in the rearing of the offspring correlates to some extent with group structure. Male care of the young is found in all monogamous species, although the extent to which this behavior is exhibited varies between species and even between groups of the same species (Carpenter, 1940; Chivers, 1971, 1972; Crandall, 1951; Ellefson, 1968; Epple, 1975; Fox, 1972, 1974; Ingram, 1977; Mason, 1966; Moynihan, 1964; Redican, 1976; Sanderson, 1957). In polygynous groups where only one male is present together

with several females and offspring, male parental behavior ranges from quasimaternal behavior, as seen in hamadryas males (Papio hamadryas) (Jolly, 1972; Kummer, 1971) and in gelada males (Theropithecus gelada) (Bernstein, 1975) to that of a distant protector, such as the patas male (Erythrocebus patas) which seldom directly interacts with infants (Hall, 1965).

In polygamous groups, which consist of more than one mature male and more than one mature female and offspring, the range of male parental care equals that in polygynous groups. Thus, for example, rhesus males (Macaca mulatta) generally ignore infants (Southwick, C.H., Beg, M.A., & Siddiqi, M.R., 1965), or interact aggressively with them (Lindburg, 1971), while in Japanese macaques (Macaca fuscata) (Itani, 1959) and Barbary macaques (Macaca sylvana) (Deag and Crook, 1971) male care of infants was described as similar to maternal care.

2. Related Studies on Alouatta

A great number of studies have been done on Alouatta palliata on Barro Colorado Island in Panama, while very few studies have ever been undertaken with Alouatta seniculus or other species of the genus Alouatta within Central and South America. Apart from ecological studies (Bramblett, 1976; Coelho et al., 1976; Schlichte, 1975), the social behavior of Alouatta palliata pigra of Guatemala has not received much attention, and it has never been studied in Belize.

Carpenter (1934), who undertook the first systematic fieldwork on howlers on Barro Colorado Island in Panama, pointed to some very deep-seated characteristics which were confirmed in later studies. These are a high degree of integrity within groups and great intragroup

tolerance, but agonistic behavior between groups, relatively stable groupings within respective areas, and loose dominance hierarchies.

The great plasticity found in grouping and leading tendencies of Alouatta palliata in response to external stress was studied by Baldwin and Baldwin (1976), Chivers (1969), Collias and Southwick (1952), Heltne, Turner and Scott (1976), Mittermeier (1973), and others. Collias and Southwick (1952) found that after a yellow fever epidemic that raged through Panama in 1951, males were redistributed throughout the troops and female leadership was common. Neville (1972a) also commented on female leadership in polygamous troops in Venezuela.

These studies suggest that grouping patterns in Alouatta are plastic enough to change as this becomes necessary for survival. Chivers (1969) proposes that the eventual splitting into more but smaller groups subsequent to population increase is an adaptive spacing mechanism developed by Alouatta in response to population pressure. Although this explanation may pertain to the case of the yellow fever epidemic, it does not answer the question regarding the extent to which grouping tendencies of Alouatta in undisturbed areas are affected by ecological or social factors. We do not know why Alouatta palliata is generally found in large troops throughout Panama, while Alouatta seniculus occurs in small to intermediate groups in Venezuela (Neville, 1972b) and in small troops throughout the Colombian (Klein, 1972) and Peruvian jungle. The groups of Alouatta seniculus which I encountered in the tropical rainforest in Peru during a survey (fall 1977) ranged from two to five animals. It is also not known why we find small monogamous groups of Alouatta palliata pigra in Tikal where according to Bramblett (1976) and Coelho et al. (1976), food supply is plentiful and

thus not a limiting factor on group size. As is the case in Tikal, the groups of Alouatta palliata pigra in Belize also exhibit the monogamous grouping pattern, ranging from two to seven animals per group.

3. Parental Behavior in Alouatta

The fact that Alouatta occurs in monogamous, polygynous, and polygamous groups suggests that parental behavior might take different forms within the various grouping patterns.

Parental behavior has never been studied in captive howler monkeys. This lack is due mainly to the fact that it has always been very difficult to keep individuals or groups of howlers in captivity, with the exception of the Frankfurt Zoo, where a group of four individuals has been kept for several years and where I had a chance to observe interactions between group members for 70 hours.

Observations on parental behavior in feral howlers find general agreement among investigators (Altmann, 1959; Baldwin and Baldwin, 1973; Carpenter, 1964, 1965; Neville, 1972a), and differ only in minor instances which are within the range of normal intraspecific behavioral variations.

All studies on parental care in Alouatta refer to the close mother-infant bond and the accommodative behavior of the mother toward her offspring (Altmann, 1959; Baldwin and Baldwin, 1972; Carpenter, 1964; Neville, 1972a). The mother is considered the core of the group (Carpenter, 1964), with a subgroup forming around her usually consisting of an infant and a juvenile, while other individuals only temporarily associate with them (Altmann, 1959; Carpenter, 1964). The other individuals are usually composed of adult and sub-adult females and

juveniles who tend to stay close together.

Male-infant relationships have not been documented to any degree in the howler literature, and seem to be generally rather loose. With regard to very young infants, Neville's (1972a) observations in Venezuela agree with those of Carpenter (1964) and Baldwin and Baldwin (1973) in Panama in that the males usually show no reaction to, nor curiosity in, these young group members. They exhibit, however, a fairly high degree of tolerance towards young infants, and react positively in unusual situations. Thus, a male retrieved and carried on his back a fallen infant whose mother had been shot (Carpenter, 1964).

Carpenter (1965) observed that the young animals constantly orient themselves with reference to the adult males, the 'leaders of the clan'. They are said to follow the males, especially during progressions, and respond to cues from them. Carpenter believes that male-young relationships supplement the integration processes of maternal relations, and play relations, and hence the social bonds of the young animals with the group are strengthened.

CHAPTER THREE

METHODS

Study Areas

Tikal / Guatemala

This study site is located at the center of the 567 km² Tikal National Park. The area is a series of low rolling hills, ranging from sea level to about 250 meters. The hills are surrounded by 'bajos', flat areas which flood during the rainy season from June to October. The lowland dry forest or quasi-rainforest - consisting of three to five stories of vegetation - receives an annual rainfall of less than 200 centimeters (Bramblett, 1976). Of the 36 species of trees which are most common in the Tikal area, the ramon tree (Brosium alicastrum) is the most abundant tree, and serves as major food source for Alouatta (Murie, 1935; Schlichte, 1975).

Primatological fieldwork in Tikal was facilitated by a network of paths and detailed maps of the physical features and archeological sites of this immense 2000 year old Mayan city. The dense vegetation, however, and the fact that the howlers were found mainly in ramon trees, which compose the upper canopy and stand between 30 and 40 meters, made visibility a major problem, and did not permit the collection of precise continuous data as was the case in Belize.

Bermudian Landing / Belize

The study was conducted in the Belice District, 60 km west of Belize City, Belize. The seven square km study area around Bermudian Landing (88° 33.7' W longitude, 17° 32' N latitude; see map page 153)

is traversed by the Belize River on the banks of which several small villages are found.

The study area lies in the Dry Tropical Lowland Zone, has a mean annual rainfall of less than 80 inches, and has a mean annual temperature of more than 24°C (Wright et al., 1959). The wet season lasts from May or June to October, and the transition from summer circulation to the winter pattern is rapid (Jenkin et al., 1976). The coolest temperatures occur between November and January (average 75°F), the warmest from May to September (average 81°F). Dense morning fogs are common from October to February on the middle and upper reaches of the Belize River. These fogs usually disperse by 9 A.M.

The region exhibits a great variety of ecological zones due to the range of elevations from 0 to 120 meters and to human disturbance of the vegetation. The howlers were found in gallery forests along the river, in the less disturbed lowland dry forest, on plantations, and on large isolated fig trees surrounded by savanna and swampy grasslands. Compared to the dense continuous upper canopy in Tikal, the vegetation in Belize is considerably shorter (10 to 15 meters) with the exception of fig trees (Ficus glabrata), which reach 40 to 50 meters. Fig trees, however, often stand isolated and mostly have sparse foliage. These circumstances and the fact that the howlers ate newly forming buds, leaving some trees virtually bare of leaves, contributed to the excellent visibility in most areas.

The howlers of Belize were usually encountered on the following trees: Ficus glabrata and Ficus sp., Achras zapote, Cecropia peltata, and Spondias mombin. They were also seen eating Acacia cookii, Acacia angustissima, and Acacia costaricensis.

Study Groups

Tikal Groups

Three groups of howlers were encountered within the 5 km² study site around the Central Plaza area at Tikal (table 1). No other groups were located during excursions outside this area.

Howling was very irregular in the howler monkeys in Tikal. Many days could pass without a single howl to indicate the location of the troops. Once located, the animals usually remained at a height of 30 meters and above. Although during feeding the howlers came as close to me as 15 meters, parental behavior, with the exception of carrying the infant, took place during resting in the dense upper canopy where little of it could be observed.

Belize Groups

Thirteen groups of howlers and two solitary males were encountered in the seven square km study area. Population density was 8.14 howlers per km² with an average group size of 4.4 animals (tables 2 and 2a). The sex ratio was 1:1. Apart from group I (polygamous grouping pattern) and group VI (polygynous grouping pattern), the remaining groups were monogamous. I refer to the black howler groups in Belize as monogamous, since of 13 groups encountered, 11 consisted of one adult male, one adult female and offspring. Why, out of a total of 16 groups of Alouatta palliata pigra encountered in Belize and Guatemala, two did not exhibit the monogamous grouping pattern, is not known. Epplé (1975) suggested that large groups encountered in the wild might occur when mature offspring leave the group, pair-bond, reproduce, and occasionally return to the original parent group. Another possibility

is that groups merged after the devastating hurricane that swept this area four months prior to the study. Local informants reported on howlers being killed during these storms. A single male which was generally found on a big fig tree across the river from group I belonged to a family of five prior to the hurricane. Single females were not seen.

Of the 13 groups encountered in Belize, only groups I to VI were studied in depth. No infants were present in groups A to G (table 2a). Nine infants were present in the six groups studied (table 2).

To what extent population density and group size are affected by disease, natural disaster, and predation is not known. The yellow fever epidemic of the early 1950's had greatly decimated howler populations in wide areas of Belize. Hurricanes took their toll on howler groups. On September 18, 1978, Hurricane Greta devastated the area, uprooting trees and killing howlers in the process. River crossings, as reported by numerous witnesses, are suspected to be hazardous to the howlers due to the strong currents in the Belize river.

Among animal predators, dogs occasionally caught howlers which were forced to descend to the ground to reach isolated trees or patches of trees. I have witnessed confrontations between iguanas (Iguana iguana) and howlers on trees. Although no physical attacks were witnessed, the howlers seemed to be apprehensive of the iguanas, while the iguanas were never seen giving way to howlers. Whether iguanas prey on young howlers is not known. Poisonous snakes such as the fer-de-lance (Bothrops atrox) and coral snakes (Micrurus sp.) abound, and boa constrictors (Constrictor constrictor imperator) have been sighted also; it is not known, however, whether they can be considered potential

enemies. Although howlers are not hunted by the local population, infants are sometimes caught and kept as pets.

Data Collection

During the three months of the field study from December 28, 1978 to March 26, 1979, 750 hours were spent in the field in Guatemala and Belize.

Tikal / Guatemala

Although the time spent in the two different study areas was roughly equal, the Tikal site yielded only 52 hours of data due to the circumstances described earlier. Differences in data collection - data in Tikal was collected in 10-minute intervals while the observation conditions in Belize allowed for data to be collected on a continuous basis - did not warrant quantitative evaluation of the Tikal data, and comparisons between the two study regions are qualitative only. Apart from different time intervals used during data collection, the same strategies were employed in obtaining data on the three groups in Tikal and the six groups in Belize as described in the following section.

Belize

Observation conditions in Belize were excellent. Very good visibility was provided by the generally low and sparse vegetation. A considerable number of groups within the study area and their habit of howling fairly regularly greatly facilitated locating the groups. Data were collected for a total of 477 hours from the six groups with young during January and February of 1979.

Our tent was close to group I, which could be observed at any time in any weather condition. After heavy rains, mainly at night,

groups II and V could not be reached due to deep mud especially at the river banks. In order to observe groups other than I, the Belize River had to be crossed by ferry, or an extensive hike was undertaken. Local people very kindly assisted me to penetrate dense vegetation using the machete, and to reach study sites by dugout canoe.

Data were collected every day on one of the groups with infants. Observations were begun at 0500 or 0600 depending on the area where the group was located. Whenever possible, I remained with each howler group for the entire day, following it on its pathways until it settled down for the night. The next day the group was contacted at dawn before it started to move.

Since only six of the thirteen groups in the study area were with young and each group differed from every other one in its age-sex composition, identification of the six groups under observation presented no problems. Only the home ranges of groups IV and VI overlapped.

Due to the small size of the groups and the heterogeneous age-sex composition within each group, identification of the individual animals was comparatively easy as well.

In some species of Alouatta, the sex determination of infants and juveniles presents a problem (Baldwin and Baldwin, 1973; Carpenter, 1965) because characteristics of the genitalia of immature animals are similar. This problem does not exist in Alouatta palliata pigra in Tikal and Belize. The testes in even the smallest male infants observed were fully descended and conspicuously white in colour.

In placing the howler infants into age categories, the estimates devised by Carpenter (1965) were used (table 3). My own observations of a ten months old red howler infant (Alouatta seniculus) at the

Frankfurt Zoo and the precise age determination of the six months old female infant and the four months old male infant of group I (ages at beginning of study), as indicated by informants living close by and a film maker who included the group in a wildlife documentary during the time when the infants were born, were helpful in the determination of ages. In accordance with Neville (1972b), I judged subadult females by their intermediate size and the intermediate state of the external female genitalia (lasting approximately one year), as well as by their more playful behavior. In agreement with Neville (1972b), subadult males could be recognized by their somewhat smaller size compared to the adult male, their less extreme development of head and throat anatomy, and their tendency to play more and engage less in the characteristic howling in response to certain stimuli.

The kind, frequency, and duration of interactions between infants and other group members have been used as indicators of parental behavior. Although certain types of interactions do occur between two animals which are at a distance, in this study only interactions involving body contact were considered. For example, a female with her infant frequently sat down close to a male. In this case the proximity between the male and the infant was caused by the female and thus does not reveal any intentions of either male or infant.

Data were recorded within each group using the Focal Animal Sampling Method (Altmann, 1973). This method lends itself well to questions requiring kind, frequency, and duration of interactions. The recording of transition times (i.e., onsets and terminations) preserves frequency and sequence information as well as the time spent in various interactions.

The infant was considered the Focal Animal within each group. It provided a complete record of all parental behavior as it initiated and received interactions. Where more than one infant was present, each infant was considered a focal animal, or, where the activities allowed for it - playing together or both resting in close vicinity - two focal animals were observed simultaneously. Each infant's interactions with the physical (non-social) environment were also recorded to shed light on its degree of independence and to allow for the compilation of a complete behavioral profile of each infant under study.

The favorable conditions for observation made it possible to collect data on a continuous basis. I found that the practice of taking continuous data minimized sampling biases, since activities throughout the day were evenly represented. Weather conditions, however, may have somewhat biased my results, since small infants are not active during rainy and windy periods. Only group I was observed during a few hours of inclement weather, and this fact should not greatly distort the considerable amount of data secured from group I.

A tape recorder was used to record quantitative and qualitative data during times of great activity. During resting periods, data was directly transcribed on data sheets (p. 150) by two assistants.

The beginning and the end of interactions of each focal animal were recorded in minutes divided into decimals. Initiator, recipient, and terminator of each interaction involving the focal animal were noted. Different codes were used for each type of activity (pp. 151,152). Stimuli that appeared to be responsible for a particular behavior, and the general context that could have evoked the behavior were recorded (Baldwin and Baldwin, 1973).

Apart from the infants' social and non-social interactions, data on troop composition, order of troop progression, location, tree types, intra- and inter-specific encounters, vocalizations, and weather conditions were recorded. Also the circumstances leading to an interaction were noted. Interactions which could not be seen properly were not recorded. For this reason, 'nursing', although a frequent interaction between mother and infant, was categorized with 'clinging ventrally'. In most cases it was impossible to see whether the infant was still nursing or had fallen asleep and was just clinging to the mother. For small infants the category 'feeding' was not used, since infants played with or playfully nibbled at the leaves more than they ingested them.

Behavioral observations were made with the unaided eye where possible, otherwise with Bushnell 7x35 binoculars. Slides were taken with an Olympus 35 mm SLR camera mounted with a 280 mm telephoto lens.

Analysis and Presentation of Data

The quantitative data consist of two major categories:

1. Social interactions involving an infant and other group members (table 4).
2. An infant's interactions with its physical environment (table 4a).

The specific types of interactions recorded are presented in the ethogram on pages 151, 152. Due to the virtual absence of agonistic interactions - two among a total of 3138 interactions - they have not been analyzed and are not included in the above categories.

The great diversity of the types of recorded behaviors made

it impossible to present them all independently. Therefore they are either lumped into one single category or assigned to broad classes of behavior - clinging, affiliative interactions (affiliation), and play (table 4). Frequencies and duration of behaviors were obtained through SPSS (Statistical Package for the Social Sciences) Computer Runs.

The data are presented in three major sections: 1. The Individual, 2. the Age Class, 3. The Species.

The Individual

In this section the emphasis is on inter-individual variability among infants relative to the parental behavior they solicit and receive. The data are presented in two different manners showing

1. an individual behavioral profile of each infant
(tables 5 to 10),
2. patterns of interactions between each infant and its
respective group members (tables 11 to 28).

1. The individual behavioral profile of each infant indicates the extent to which each infant engaged in social and non-social interactions. In this presentation, the various types of interactions are treated as a single category. Emphasis is placed on both the frequency and the duration of interactions. Percentages for the frequency of dyadic interactions (Mo-I, M-I, etc.) are derived from the total sum of all interactions recorded during the study on the particular focal animal. Thus, for example, the percentage for the MI_1 - Mo dyad in group III was derived as follows:

$$\frac{92}{144} \quad \begin{array}{l} \text{(number of interactions with mother)} \\ \text{(total number of interactions involving focal animal)} \end{array}$$

= 63.9 %. Thus 63.9 % of all interactions involving the infant took

place between the infant and its mother (table 5).

Percentages for the total duration of interactions were based on the entire time the infant was under observation. The formula for this calculation is as follows: (example taken from the MI_1 -Mo dyad, group III; see table 6)

$$\frac{1443.1}{1684.7} \begin{array}{l} \text{(minutes of } MI_1\text{-Mo interactions)} \\ \text{(total time of observation on } MI_1 \text{ in group III, in minutes)} \end{array}$$

= 85.7 %. The infant passed 85.7 % of the observation time in close physical association with its mother.

In this presentation, the individual behavioral profile of each infant is compared to the behavioral profiles of the other two infants within each age class.

2. Patterns of Social Interactions.

In this section an infant's interactions with the physical environment are not included. This presentation emphasizes not only how often and for how long an infant engaged in interactions, as seen in the behavioral profile, but it also shows the types of interactions which occurred within the dyads. In order to present the data in a more coherent fashion, specific interactions as listed in the ethogram were assigned to broad behavioral categories - Clinging, Affiliation, and Play (table 4). The categories were devised in consideration of the forces - life-sustaining, affiliative, playful - which brought the animals together in interaction.

CLINGING includes four separately recorded behaviors - clinging ventrally and dorsally while support animal (usually mother) is at rest, and clinging ventrally and dorsally while support animal moves. Clinging is considered a life-sustaining type of interaction, because a small infant must cling to its mother for warmth, support and nutrition.

The category AFFINITIVE INTERACTIONS consists of the behaviors: sitting in close body contact, grooming, hugging, huddling, muzzling, and touching. These interactions are not directly important for survival. Although affiliation may be inherent in clinging or play interactions, it is not considered the primary motivator in these behavioral categories, as it is in affinitive interactions.

The PLAY category incorporates the following behaviors: following in close body contact (considered a play invitation - usually performed with a bouncy gait), playing - with both animals active, playing with part of the other animal's body, and climbing across another animal's back (also considered a play invitation, since this was usually done in a playful manner). Although, as was stated before, it was not ruled out that the animals show affiliation when playing, play does incorporate other elements. Playing is often done in an exuberant manner, sometimes bordering on rambunctiousness. Play also incorporates the element of exploration. Young howlers are frequently engaged in the exploration of another animal's body or the environment.

Tables 11 to 28 show row, column, and total percentages for each category of behavior between an infant and each of its group members. Thus, for example, the row percentage of Clinging in the mother-infant dyad in group III (table 11) was derived as follows:

$$\frac{61}{65} \left(\frac{\text{number of clinging interactions between infant and mother}}{\text{total number of clinging interactions that occurred in group III}} \right) = 93.8 \%. \quad 93.8 \% \text{ of all clinging interactions took place between infant and mother.}$$

The column percentage was based on all interactions - clinging, affiliation, play - that took place between the mother and her infant.

$\frac{61}{92}$ (number of clinging interactions between infant and mother)
 (all interactions between infant and mother)

= 66.3 %. Clinging amounted to 66.3 % of all interactions that occurred between mother and infant.

The total percentage was based on all interactions that took place between the MI_1 in group III and all members of this group.

$\frac{61}{138}$ (number of clinging interactions between infant and mother)
 (all interactions between infant and other group members).

= 44.2 %. This figure means that 44.2 % of all kinds of interactions that occurred between the infant and all other group members pertained to clinging to its mother.

Similarly, calculations were done to obtain percentages on the duration of interactions. The base used was the elapsed time (in minutes) of interactions between the focal animal (infant) and other group members.

Rather than going systematically through all the data presented in tables 11 to 28, I shall point to specific examples which illustrate the variety of ways in which inter-individual variability manifested itself and which most clearly characterized the dyads in question. The patterns of interactions of each infant are presented in comparison with those of the other two infants of each age class, underlining the extent of individual variability among infants.

The Age Class

Here the data are presented at a more generalized level. The infants are categorized into the three different age classes. Emphasis is on the type of change which took place with age of the infants.

The behavioral profiles (tables 29-32) are averages for an

age class. Group members other than the mother are lumped into a single category to identify the trend with age away from the mother toward other group members or toward interactions with the physical environment, as postulated at the beginning of the study. Changes in adult male - infant interactions are treated separately, since one of the primary interests of this study is the nature of male parental care.

Another change in parental behavior relating to the maturing offspring is sometimes seen in the process of peripheralization. In this process, the offspring is gradually pushed away from the group in a process which is essential if the monogamous grouping pattern is to be maintained. Table 33 presents data relating to this process that have been calculated from tabulations from computer runs. The percentage of terminated interactions within each age class are derived as follows:

$$\frac{42}{1145} \begin{array}{l} \text{(number of interactions initiated by the infant and} \\ \text{terminated by other group members)} \\ \text{(total number of interactions initiated by infant)} \end{array}$$

= 3.7 %. That is, of the 1145 interactions which were initiated by infants of age class I, 42 or 3.7 % were terminated by group members other than the infant.

The Species

Here the data are treated at yet a higher level of generality and abstraction with the intent to compare general parental behavior patterns as they occurred in howler troops in Belize with those in other species, especially those in monogamous groups.

The mean behavioral profile of a howler infant was devised by lumping all interactions which occurred between an infant and its respective group members in the six groups under study (tables 34, 35).

Interactions with the physical environment were lumped as well. Patterns of interactions as they were presented for each individual animal (tables 11 to 28) were also lumped within each dyad and each type of interaction - Clinging, Affiliation, Play (tables 37, 38).

The frequency at which an infant on the average initiated, received, and terminated interactions was summarized in table form and expressed in proportions (table 38).

CHAPTER FOUR

THE INDIVIDUAL

RESULTS

Infants of Age Class I

1. Individual Behavioral Profiles

Although all three infants were assigned to age class I, there was a discrepancy in age between the MI_1 (for abbreviations see table 1a) of group III which was approximately two months old at the beginning of the study, and the other two infants of this age class which were four months old. The two four months old infants - although still somewhat uncoordinated - were able to locomote on their own, while the infant in group III was largely restricted to movement on the body of a group member.

Interactions with the mother

Tables 5 and 6 show that the MI_1 in group III interacted much more frequently with its mother (63.9 %) and for longer periods of time (85.7 %) than either the MI_1 in group I (41.9 % for frequency, 72.8 % for duration) or the MI_1 in group VI (35.4 % for frequency, 52.7 % for duration).

Interactions with the adult male

Interactions among male-infant dyads within this age class differed regarding both frequency and duration. Contact between the adult male and the MI_1 in group III was characterized by few and short lasting interactions (4.9 % for frequency, 0.4 % for duration; tables 5 and 6). The value for the interactions between infant and adult

male in group I may be inflated (9.5 % for frequency, 2.6 % for duration), since two adult males were present in this group which were not individually recognized at all times. The infant was never seen interacting with both males simultaneously, and it is not known whether fewer male-infant interactions would have occurred if only one male was present. For this reason I did not divide the value by two. The male-infant bond in group VI (6.8 % for frequency, 1.5 % for duration) was intermediate in relation to groups I and III.

Interactions with females

(Females: AF, FJ₂, and FJ₁ were lumped). No female other than the mother was present in group III. For this reason, only groups I and VI can be considered. The discrepancy in the proportion of infant-female interactions among the infants of group I and group VI (tables 5, 6) may be due to the MI₁ in group I having only one adult female to contact, while the MI₁ in group VI was able to associate with three females (1 AF, 1 FJ₂ and 1 FJ₁). Again, it is not known to what extent the number of animals within a certain category - in this case females - affected the total frequency of interactions with the infant.

Interactions with peers

Each of the infants of age class I had one peer to associate with. In group III interactions took place between the MI₁ and the MI₃, in group I between the MI₁ and the FI₂, in group VI between the MI₁ and the MI₂. Table 6 indicates that the values are very close for the total time each infant spent interacting with a peer (10.6 % group III; 10.2 % group I; 10.0 % group VI). With regard to the frequency with which interactions were carried out, a considerable discrepancy between infants is apparent. In group III, 27.1 % of all interactions took

place among the two infants, while in groups I and VI the values are 16.0 % and 8.9 % respectively (table 5). Thus each contact between the MI_1 and the MI_3 in group III was much shorter than contacts between the MI_1 and its peer in group I. Contact was longest between the infants - MI_1 and MI_2 - in group VI.

Interactions with the physical environment

In both frequency and duration of non-social interactions, the MI_1 in group III rated very low (4.2 % for frequency, 3.3 % for duration) (tables 5, 6). A considerable difference is also apparent between the two infants in groups I and VI. The MI_1 in group VI spent more than twice as much time away from group members (27.4 %) than did the MI_1 in group I (12.1 %) (table 6).

To examine whether the variability is statistically significant, the following null hypothesis was tested:

There is no significant difference among the individual behavioral profiles of the three infants of age class I.

The Kolmogorov-Smirnov two sample test ($\alpha = .05$) yielded significant differences both regarding the frequency and duration of interactions between the behavioral profiles of the infants of groups I and III ($D_{\max} = .221$, $D_{.05} = .122$), I and VI ($D_{\max} = .180$, $D_{.05} = .108$) and III and VI ($D_{\max} = .396$, $D_{.05} = .150$), for frequency. For duration, the values were as follows: groups I and III ($D_{\max} = .129$, $D_{.05} = .036$); groups I and VI ($D_{\max} = .211$, $D_{.05} = .039$); groups III and VI ($D_{\max} = .329$, $D_{.05} = .049$). The null hypothesis was rejected for both frequency and duration in all three groups. Thus, the individual behavioral profiles differ significantly among the three infants of age class I.

2. Patterns of Social Interactions

Clinging

A certain type of interaction can be restricted to an infant and just one particular group member, or it can take place between an infant and several group members (tables 11 to 16). Thus, for example, the MI_1 in group VI clung only to its mother, while the infants in groups I and III occasionally also clung to other animals in the group. There is a difference of roughly 10 % in the frequency with which each of the infants of age class I engaged in clinging interactions (tables 11, 13, 15 - total column).

Affinitive Interactions

Although affinitive interactions occurred among infants and all other animals in groups III, I, and VI, in this behavior the MI_1 in group I interacted most frequently with its mother (60.4 %, table 13), while in group III the closest affinitive tie existed between the MI_1 and the MI_3 (frequency of 58.5 %; table 11). In group VI a little less than half of the affinitive behavior occurred between the MI_1 and its mother (46.3 %), while somewhat more than half took place between the infant and other group members (53.7 %), predominantly the adult female (19.5 %) and the adult male (17.1 %; table 15). The values in the tables indicate that the most frequent type of behavior that occurred in infant-adult male dyads (culminating in 26.9 % for frequency in Group I), was that of affiliation.

Play Interactions

In group III the MI_1 played about equally frequently with its mother (48.2 %) and the MI_3 (46.4 %) (table 11). The play bouts with the mother, however, lasted longer (67.6 %) than those with the MI_3

(31.1 %) (table 12). In group I, the MI_1 played more frequently with the FI_2 (47.2 %) than with its mother (25.2 %) (table 13). Here, however, the play bouts between the infants lasted considerably longer (65.8 %) than those between mother and infant (15.1 %) (table 14). In group VI the MI_1 played slightly more often with the MI_2 (34 %) than with the mother (30.0 %) (table 15); the play bouts, however, lasted much longer when the infants played (61.8 %) than when the mother participated in the play (19.6 %) (table 16).

Infants of Age Class II

1. Individual Behavioral Profiles

The three infants of age class II were six months old at the beginning of the study. They were of the same size and at the same level in locomotor skills. The infants of this age class were well coordinated; the jerky movements seen in the infants of age class I were never observed in these infants.

Interactions with the mother

A smaller difference was detected among the infants of age class II in the frequency with which each infant interacted with its mother than was found in age class I (table 7). Regarding the duration of interactions, close agreement existed only in the mother-infant dyads in groups V (48.6 %) and VI (45.3 %), while the FI_2 in group I spent considerably more time in association with its mother (62.6 %) (table 8). A comparison of the frequency and duration of interactions between the infants in groups I and V revealed that although the FI_2 in group I interacted less frequently with its mother (33.8 %) than the MI_2 in group V (37.5 %), it interacted for a longer total period of

time (62.6 % versus 48.6 % for the MI_2 in group V; tables 7, 8). The MI_2 in group VI associated least with its mother for both frequency and duration of interactions (table 7, 8).

Interactions with the adult males

There were two adult males in group I for the FI_2 to interact with. A rather homogeneous pattern emerged with regard to the frequency of male-infant interactions among the three dyads under consideration (table 7). The duration of male-infant interactions, however, was more variable (table 8). The MI_2 in group VI associated less frequently with the male (10.3 %) and for a shorter total time period (1.9 %) than either of the other two infants. A comparison between the FI_2 in group I and the MI_2 in group V shows that the FI_2 in group I interacted most frequently with the male (12.8 %) but for a shorter total time span (3.7 %) than did the MI_2 in group V, which interacted less frequently with the adult male (10.8 %) but associated with him for a greater total time period (4.6 %).

Interactions with females

Females (AF , FJ_2 , and FJ_1) are lumped in this analysis. There is little discrepancy in the proportions of the frequency with which female-infant interactions occurred in groups I (7.4 %) and V (8.2 %) (table 7). The proportion of female-infant interactions in group VI, however, is considerably greater (12.8 %) (table 7). There were three females in group VI as compared to only one each in groups I and V, a fact which may account for the discrepancy. Regarding the duration of interactions, the MI_2 in group VI spent more time with the females (5.4 %) than either the MI_2 in group V (4.8 %) or the FI_2 in group I (2.6 %) (table 8).

Interactions with peers

The MI_2 in group V did not have a peer and cannot be considered in this analysis.

Table 7 indicates that the FI_2 in group I associated slightly more than twice as often (15.4 %) with its peer than the MI_2 in group VI (7.4 %). Regarding the duration of peer interactions, there is little difference between group I (8.8 %) and group VI (8.4 %), a result which demonstrates that although the MI_2 played less often with its peer, the play interactions lasted almost twice as long as peer interactions in group I.

Interactions with the physical environment

There is close agreement in the patterns of non-social interactions between the MI_2 of group V and the MI_2 of group VI. Each of these infants spent almost twice as much time in non-social interactions as the FI_2 in group I (tables 7, 8).

The individual behavioral profiles of the three infants of age class II differ in many aspects. To test whether this variability is statistically significant, the following null hypothesis was proposed:

There is no significant difference among the individual behavioral profiles of the three infants of age class II.

The Kolmogorov-Smirnov two sample test ($\alpha = .05$) yielded significant differences in the duration of interactions between the individual behavioral profiles of the infants of group I and V ($D_{\max} = .25$, $D_{.05} = .04$), I and VI ($D_{\max} = .21$, $D_{.05} = .04$), and V and VI ($D_{\max} = .07$, $D_{.05} = .05$). Regarding the frequency of interactions, significant differences were obtained in the behavioral profiles of

the infants in groups I and V ($D_{\max} = .21$, $D_{.05} = .10$), and I and VI ($D_{\max} = .20$, $D_{.05} = .10$). No significant difference was obtained in the frequency of interactions in the behavioral profiles of the infants of group V and VI ($D_{\max} = .11$, $D_{.05} = .13$). Thus, the null hypothesis was rejected for all cases except for the frequencies of interactions between the behavioral profiles of the MI_2 in group V and the MI_2 in group VI.

2. Patterns of Social Interactions

Clinging

The MI_2 in group VI only clung to its mother, while the FI_2 in group I and the MI_2 in group V occasionally clung to other group members (tables 17-22). The FI_2 in group I spent more than half of the total number of interactions (55.1 %) that occurred within this dyad (see column percentage, table 17) clinging to its mother. This type of interaction was less pronounced between the MI_2 and its mother in group VI (36.5 %) and between the MI_2 and its mother in group V (34.5 %) (tables 17, 19, 21). The same pattern appears in the duration of clinging interactions as they are seen in the mother-infant dyad. Again the FI_2 associated for a longer period of time with its mother (86.1 %, column percentage table 18), followed by the MI_2 in group VI (70.3 %), and the MI_2 in group V (68.8 %).

Affinitive Interactions

This type of interaction occurred between infants and all other group members. All three infants spent the greatest proportion of affinitive interactions with their mothers (tables 17 to 22). In group I, the affinitive bond between the FI_2 and the adult males was

close (33.4 % for frequency, 15.7 % for duration; tables 17, 18). Weaker affiliative ties existed between the MI_2 in group VI and the adult male (22.4 % for frequency, 7.7 % for duration; tables 21,22). In group V affiliation was slightly stronger between the MI_2 and the FJ_2 (20 % for frequency, 16.8 % for duration) than between this infant and the adult male (16.4 % for frequency, 14.7 % for duration; tables 18, 19). The column percentages show that of male-infant interactions, affiliation was most common (tables 17 to 22).

Play

Play interactions took place between infants and all other group members (tables 17 to 22). It was, however, most prevalent among peers, especially regarding the duration of play interactions (59.4 %, group I; 59.6 %, group VI; tables 18, 22). In group V where no peer was present, play interactions occurred almost equally frequently between the MI_2 and its mother (45.5 %) as between the MI_2 and the adult male (42.4 %, table 19). Play in this group, however, lasted longer between mother and infant (46.9 %) than between the adult male and the infant (29.2 %, table 20). Play activities between the MI_2 and the FJ_2 in group V - although less frequent than among the other dyads (12.1 %, table 19), show an increase in duration (24 %, table 20). Regarding peer interactions, the column percentages of tables 17, 18, 21, and 22 indicate a consistently high proportion (in the 90 % range) of play.

Tables 17 to 22 indicate that despite some similarity in the patterns of social interactions of the three infants of age class II, individual variability prevails.

Infants of Age Class III

1. Individual Behavioral Profiles

The three infants of age class III were very close in size, and thought to be about 12 months old, based on comparison with a 10 months old FI₃ in the Frankfurt Zoo, Germany and descriptions of howler infants by Baldwin and Baldwin (1973). These infants no longer nursed and locomoted independently at all times.

Interactions with the mother

Table 9 indicates that the proportions of the frequency of mother-infant interactions differ little between the three infants of age class III. There is also little difference in the percentages of the duration of mother-infant interactions in group II (23.3 %) and III (22.6 %). The MI₃ in group IV, on the other hand, spent a greater porportion of time with its mother (34.7 %, table 10).

Interactions with the males

There were two males in group IV (1 AM, 1 MJ₂). Male-infant interactions were most frequent in group IV, amounting to 28.3 %. Contact was considerably less frequent between the MI₃ and the adult male in group III (8.4 %), and least between the FI₃ and the adult male in group II (4.1 %). The situation differed regarding the duration of interactions. The longest lasting contact existed between the MI₃ and the adult male in group III (24.9 %), followed by interactions between the MI₃ and the males in group IV (19.7 %). The FI₃ in group II spent little time interacting with the adult male (0.8 %, table 10).

Interactions with females

No female other than the mother was present in group III.

Table 9 illustrates that more frequent interactions occurred between the MI_3 in group IV and two females (FJ_2) (9.8 %) than between the FI_3 in group II and one female (FJ_2) (6.2 %). Regarding the duration of the contact, the discrepancy is even greater. The MI_3 in group IV spent more than three times as much time with the females (12.6 %) as the FI_3 in group II (3.8 %).

Interactions with peers

Only the MI_3 in group III had a peer with which to interact with. The MI_3 in group III interacted frequently (29.5 % of all interactions) and for short periods of time (9.2 %) with the MI_1 .

Interactions with the Physical Environment

The FI_3 in group II interacted more frequently (59.8 %) and for a longer period of time (72.1 %) with the physical environment than either the MI_3 of group III (37.9 % for frequency; 43.3 % for duration) or the MI_3 of group IV (34.6 % for frequency; 33.0 % for duration).

To determine whether the variation that was found in the individual behavioral profiles of the three infants of age class III is statistically significant, the following null hypothesis was tested:

There is no significant difference among the individual behavioral profiles of the three infants of age class III.

The Kolmogorov-Smirnov two sample test ($\alpha = .05$) yielded significant differences for the frequency of interactions between the individual behavioral profiles of the infants of group II and III ($D_{\max} = .30$, $D_{.05} = .20$), III and IV ($D_{\max} = .25$, $D_{.05} = .17$) and II and IV ($D_{\max} = .25$, $D_{.05} = .17$). Regarding the duration of interactions, significant differences were obtained for the behavioral profiles of the infants of group II and III ($D_{\max} = .33$, $D_{.05} = .05$), III and IV

($D_{\max} = .13$, $D_{.05} = .04$), and II and IV ($D_{\max} = .39$, $D_{.05} = .04$).

The null hypothesis was rejected in all cases.

2. Patterns of Social Interactions

Clinging

The few clinging interactions that still occurred among infants of this age class were restricted to the mother-infant dyad in group II, while in groups III and IV the infants occasionally clung to group members other than their mother (tables 23-28). The values indicate that the FI_3 in group II was clinging less to its mother than the MI_3 s in groups III and IV.

Affiliation

Infants engaged more frequently in affiliative interactions with their mothers than with other group members (tables 23, 25, 27). For duration, however, this outcome is pronounced only in the mother-infant dyads in group II (84.1 %) and IV (50.5 %), while in group III the MI_3 spent more time interacting affiliatively with the adult male (61.9 %) than with its mother (36.6 %) (tables 24, 26, 28).

Tables 23 to 28 (column percentage) indicate that the increase in affiliative behavior in the three mother-infant dyads is related inversely to the decrease of clinging interactions.

The greatest proportion of male-infant interactions is of the affiliative type (tables 23 to 28). In group II all interactions between the adult male and the FI_3 related to affiliation.

Play

Only one infant was present in groups II and IV. In group II, play occurred only between the FI_3 and the FJ_2 . The infant never played

with either mother or male. In group III, play activities were most prominent between the MI_3 and the MI_1 (90 % for frequency; 88.7 % for duration), while in group IV play activities were most frequent between the MI_3 and the MJ_2 (45.8 %, table 27), but lasted longest between this infant and its mother (59.8 %, table 28).

As was the case among infants of age classes I and II, the patterns of social interactions of the three infants of age class III were characterized by great inter-individual variability.

Summary of Results - The Individual

Differences in the individual behavioral profiles of the infants within each of the three age classes were statistically significant (Kolmogorov-Smirnov two sample test, $\alpha = .05$) in all cases except for the frequency of interactions between the MI_2 in group V and the MI_2 in group VI.

Patterns of social interactions showed great variability but revealed certain common trends. Clinging interactions characterized all mother-infant dyads within age class I. Among infants of age class II, predominance in this type of behavior was seen only in the FI_2 in group I. In age class III clinging was weakly represented in all mother-infant dyads (tables 23 to 28).

Affinitive interactions were observed between infants and all other group members. This type of behavior occurred predominantly between mother and infant; in some instances, however, it found its strongest expression in the male-infant dyad (tables 23 to 28).

Play behavior varied considerably among dyads with the exception of peer relationships, where play consistently accounted for

an overwhelming proportion of interactions (tables 23 to 28).

Interactions with the physical environment varied greatly among infants of all age classes in both frequency and duration (tables 5 to 10). A trend toward an increase in non-social interactions is apparent in older infants.

DISCUSSION

As Seyfarth, Cheney, and Hinde (1978) and others regard the study of inter-individual relationships as a basic prerequisite for the understanding of the dynamics of social structure, I believe that in order to understand the principles of parental behavior in a species, it is important to know how it is achieved on the individual level. Individuals are both the products and the producers of societies (Mason, 1976). This concept relates directly to the present study, where each infant was not only affected by parental behavior, but at the same time, through its unique 'personality', exerted influence on the way parental behavior was administered. This interrelationship, which is essential to the understanding of parental caretaking patterns, is discussed in relation to the situation (age-sex composition, group strategies, etc.) as it existed within each group of black howler monkeys in the Belize area. The following discussion highlights each individual infant, comparing trends in its patterns of interactions with those of the infants within the same age class, and with corresponding reports from the literature. The quantitative data from the results section are supplemented by qualitative observations.

1. Infants of Age Class I

Male Infant₁ - Group III

Group III was composed of 1 AM, 1 AF, 1 MI₃, and 1 MI₁. The home range, which extended several kilometers west from the banks of the Belize River (see map p. 153), consisted of relatively undisturbed high forest. Other howler groups ranged close to this area, none however, contained infants.

Interactions with the mother

The mother-infant bond was a very close one, largely characterized by clinging interactions (tables 11, 12). The infant was still very dependent on the mother for frequent nursing and thermoregulation. Only during warm and calm periods of the day did the infant detach itself from the mother's ventrum in order to explore the close environment from her back. The lack of coordination in the MI₁ did not allow for complex interactions even while on the mother's back. This observation agrees with Neville's (1973a) and Shoemaker's (1979) reports on the poor coordination of 7 to 8 week old infants.

When the MI₁ detached itself from the ventral position on its mother, it clung sideways or dorsally. The infant sometimes used its tail when locomoting on the mother, wrapping it around parts of her body. Proper use of the tail, however, as seen in the older infants of this same age class was not yet detected in this young animal. Neville (1972a) reported good use of the tail in Alouatta seniculus at approximately 10 weeks.

Riding positions were at times awkward. When clinging ventrally, the infant was seen in a very forward position, holding onto the mother's neck with its hands. Sometimes it was clinging to the mother's side or

to one leg when she was walking. Similar positions for the infants were reported by the Baldwins (1973).

Affinitive behavior was rare between mother and infant (tables 11, 12). It seemed that the infant was still too preoccupied with clinging to the mother and trying to keep its balance when moving on her body in order to engage in more complex types of interactions. I assume that affinitive behavior is more frequently initiated by the infant as it becomes more coordinated. It may also be possible that an infant needs more time to develop a larger behavioral repertoire. The Baldwins (1973) and others have never observed mothers to direct overtly affinitive behavior toward their tiny infants. This observation does not agree with the mother-infant relationship under discussion. Although affinitive behavior was rare, it did occur between the mother and the two-months old infant, and was seen more frequently between mothers and somewhat older infants of age class I.

Play interactions occurred only when the mother was resting. The infant mainly played in an exploratory way, investigating parts of the mother's body - hair, ears, eyes, and tail. The mother patiently tolerated all of the infant's manipulations without retaliation, including the infant's attempts to poke into her eyes with its tiny fingers. The mother was very permissive as well regarding interactions between the young MI_1 and his older sibling, the MI_3 . She left the small infant with his older sibling while moving a short distance away. Twice she was seen leaving the MI_1 with the MI_3 while she hurried off into the uppermost canopy to howl with the adult male.

Interactions with the adult male

Contact was rare and of short duration between the tiny infant

and the adult male, consisting primarily of affiliative and play interactions (tables 11, 12). They generally occurred when the mother was settling down close beside the male or vice versa. The infant either transferred to the male's back or interacted with the male - muzzling or touching - while still partially on the mother's body. The male was very tolerant of the infant's approaches, and also initiated interactions such as touching the infant. This observation is in contradiction to most reports from other studies about Alouatta (Baldwin, 1980, pers. comm.; Didur, 1980, pers.comm.; Paterson, 1980, pers.comm.) in which adult males generally ignored small infants.

Interactions with the male infant₃

Clinging was rare and of short duration. The MI_1 was never seen resting or riding on the MI_3 . The affiliative bond between the two infants was strong, however, stronger in fact than that between the MI_1 and its mother (tables 11, 12). Play interactions were frequent among this dyad. Most of them were of the exploratory type as was the case among mother and infant. When the mother and the MI_1 were sitting in close physical contact, the MI_1 continuously moved back and forth from the back of the mother to that of the MI_3 . The MI_3 was as tolerant of the MI_1 as was the mother, allowing the infant to pull its fur or investigate parts of its body. The MI_1 was even allowed to sit on the head of the MI_3 , swishing its little tail repeatedly into the MI_3 's face. The MI_3 closed its eyes but did not move its head.

The relationship between the two infants was more reminiscent of that of an infant and its caretaker than of a peer relationship. Redican (1976) mentions caretaking behavior between infants of different ages. Also in monogamous groups of some species of New World primates

such as the brown-headed tamarins (Saguinus fuscicollis) older infants readily care for the younger offspring (Epple, 1975). For more MI_1 - MI_3 interactions, see section on infants of age class III.

Interactions with the physical environment

The small MI_1 interacted little with the environment, a fact which can be ascribed to its young age and the subsequent lack of coordination (tables 5, 6). It was sometimes standing in the foliage, clinging with only one foot to its caretaker. It manipulated leaves and branchlets, pulling and twisting them. It sometimes pulled small branches toward its body, then released them. It was never seen eating leaves, although it hesitantly nibbled on them and may have ingested some. Carpenter (1934) reported that fecal matter of two infants, which were captured when they were approximately 2 to 3 weeks old, indicated that the infants had been eating plant material.

Male Infant₁ - Group I

Group I consisted of 2 AMs, 2 AFs, 1 FI_2 and 1 MI_1 (table 2). Its small territory of only 700 m² was adjacent to the Belize River and surrounded on three sides by pastureland (see map p. 153). The group remained in this confined area for many weeks at a time. Only at the very end of the study did the troop leave the area, crossing open ground to get to the jungle about 800 meters away. The pastureland was interspersed with several trees and bushes. The males returned to the previous territory after 10 days, the females with young came back after another 4 days.

The troop slept and did most of the foraging on a huge, sparsely foliated fig tree (Ficus glabrata). Every day in the early afternoon,

the troop moved to a lower area closer to the river to rest and forage. In this area the vegetation was denser and offered shade against the hot afternoon sun. In the late afternoon the troop returned to the big fig tree.

Interactions with the mother

The mother-infant bond was very close and dominated by clinging interactions (tables 13, 14). The infant was dependent on its mother for nursing, thermoregulation, and transport. Only during the mother's resting periods or when she was foraging did the infant locomote on its own. Although the mother was sometimes seen bending down to make mounting easier for the infant, she often left it to the infant's initiative to catch up with her and cling to her body. Similar to the Baldwins' (1973) observations, this infant was seen at times to cling to one of the mother's legs, where it waited until the mother rested and then crawled to a more comfortable position. Sometimes the infant worked its way up to the mother's ventrum or back as she proceeded on her way.

The infant was repeatedly seen to use the mother's body to climb to a different spot in the vegetation. Whether it was the mother's intention to make a bridge for the infant to cross, as reported by Carpenter (1964), or whether she just happened to be there, was not always clear. The infant sometimes held onto the mother's tail while climbing in the foliage, although it was perfectly capable to move around by itself. The infant did need the mother's help, though, when large branches had to be crossed, as it tended to slip.

The mother was very permissive toward the young infant, allowing it to scoot and jump on her back, investigate her fur, or pull her tail.

She also allowed her infant to interact freely with other group members and to investigate the environment. The mother, in fact, seemed to promote interactions between her infant and other group members. Sometimes she sat down close to the adult female or one of the males with her face turned away from them. This position made it easier for the infant to transfer to the adjacent animal's back.

Considerably more affiliative behavior took place between the MI_1 and its mother in this group than was observed in group III (tables 11 to 14). Most of the affiliative interactions were initiated by the infant, although the mother was also seen approaching the infant, muzzling and hugging it.

Although the mother was seen to engage actively in play interactions (she was, for example, swinging her hand back and forth while the infant was trying to grab it), most of the play consisted of the infant exploring the mother's body or jumping on it with exuberance.

Interactions with the adult males

Although one of the adult males was slightly smaller than the other, they could not always be recognized individually unless they were close together. For this reason male-infant interactions refer to both adult males in group I.

The contact between the MI_1 and the adult males included some clinging but was mainly of the affiliative and playful type (tables 13, 14). The infant initiated most of the interactions, but contrary to many reports on male-infant interactions in other species of howler monkeys (Baldwin, 1980, pers. comm.; Carpenter, 1964; Neville, 1972a) which indicated that the male remained largely unresponsive, the adult males in group I frequently responded to the infant's approaches by

holding, hugging, or muzzling the infant. Glander (1975) also witnessed notable male-infant interactions during his study in Costa Rica. Although the males in the Belize group I were very tolerant of the rambunctious MI_1 , they sometimes moved away from the infant to find a different resting place. Great permissiveness on the part of the males was witnessed by Shoemaker (1979). He saw infants resting on males' heads and backs or hanging suspended from their long beards. The males showed no adverse reaction to this type of activity.

In group I the males were repeatedly seen to watch over an infant while the mother was absent. One such instance took place as follows:

Jan. 16, 3:15 PM: The mother sat down beside the adult male with her head turned away from him. The MI_1 transferred to the adult male ending up between his arms. The mother ran to the outermost foliage, covering a distance of about 20 meters, where she fed voraciously. The adult male held the MI_1 between his arms for over 6 minutes, muzzling him occasionally. The MI_1 then walked to the adult female who was resting at a distance of 4 meters. The female's infant - FI_2 - met the MI_1 halfway. They started rough-and-tumble play, occasionally jumping on the adult male's back. After 27 minutes of feeding, the mother returned; the MI_1 climbed immediately onto her back.

This incident is like one of Glander's (1975) observations, where a mother left her infant with a male while she was feeding; she returned after 30 minutes.

Interactions with the adult female

As compared to associations with the adult males, the MI_1 interacted less with the adult female (tables 5, 6), although it spent a considerable amount of time in her close vicinity. The infant's mother often sought close physical contact with the other adult female, whereupon the infant immediately climbed onto the adult female's back. Usually play interactions followed between the MI_1 and the FI_2 , who

sometimes sat or jumped on the female's body while playing together. The adult female (mother of FI_2), however, was never seen to carry the MI_1 while moving, whereas Glander (1975) reported on females carrying other infants in addition to their own. Otherwise, the adult female in group I extended the same degree of permissiveness to the MI_1 as to her own infant. Association between the MI_1 and the adult female was also characterized by affiliative behavior (huddling and touching) and gentle play interactions (tables 13, 14).

Alloparenting - caretaking behavior exhibited by adult and juvenile group members other than mother and adult male - was common among the females of group I. Usually the alloparent remained with both infants until the mother returned. One day, alloparenting took a different turn:

Jan. 22, 11:05 AM: The mother of the MI_1 lay down in the vicinity of the adult female. The MI_1 left his mother's back and started to play with the FI_2 around the FI_2 's mother. The mother of the MI_1 ran to the outer branches to feed, about 25 meters from where the infants were playing. The mother had been gone for 16 minutes when the female took her FI_2 on her back, leaving the small MI_1 alone high up in the tree. As the female was leaving, both adult males immediately ran to the whining infant, hovering about one meter above it, grunting. The mother hurried back from the outer branches, taking her infant on her back.

This was the only time I observed a caretaker leaving a small infant on its own. Perhaps frequent exchange of infants as it was practised among females in this group finally led to this incident.

Interactions with the female infant₂

Interactions between the infants were almost exclusively restricted to play (tables 13, 14). Play occurred either on the bodies of group members - mainly the adult females - or in the foliage. During

warm and calm weather, the infants were seen playing for hours with short interruptions, while the adults were resting or sometimes foraging. Carpenter (1965) observed that infants spent 80 % of their waking time playing. Although the MI_1 was still somewhat uncoordinated in his movements, it played exuberantly, trying to keep up with the older FI_2 . Once the MI_1 was hanging from its tail, unable to reach any part of the vegetation with its hands or feet. It fingered around nervously, trying to grasp a branchlet, but did not dare to let go by its tail. As the FI_2 came by, the MI_1 clung to her tightly, reaching the foliage with her help.

Play activities between the two infants were mostly of the rough-and-tumble type. The infants were hanging by their tails, grappling with one another, trying to pull each other down. While the infants were hanging from tails and/or limbs, they pawed at one another, and one infant often held the head of the other infant in his hands, pulling it back and forth. Chases through the foliage were common, followed by pulling of tails and limbs when the infants got close to one another and occasionally by playbiting with mouths wide open. Although play interactions were sometimes interrupted when one of the infants left to contact its mother, often for only an instant, continuous play interactions between the two infants of up to 40 minutes were witnessed.

The great permissiveness of the mothers became evident during this type of play. The MI_1 seemed to be engaging prematurely in activities of this kind as indicated by its occasional falls into the foliage. The still clumsy movements of the MI_1 testified to its relative inexperience in rough-and-tumble play activities.

Interactions with the physical environment

Roughly one fourth of the total number of interactions the MI_1 was involved in (table 5) related to the physical environment. The infant was mainly engaged in arboreal gymnastics or investigating the environment, moving through the foliage. The MI_1 swung by its tail alone, or used one or more limbs for stronger support. Manipulation of the vegetation, such as pulling on leaves and nibbling on them, did occur, but was less frequent than among older infants. This finding agrees with Baldwin's (1973) and Neville's (1972a) observations on the infants of age class I, the explorations of which were much more oriented to locomotion than to the manipulation of objects.

Male Infant₁ - Group VI

Group VI was composed of 7 animals - 1 AM, 2 AF, 1 FJ_2 , 1 FJ_1 , 1 MI_2 , and 1 MI_1 . This group ranged through high jungle area, interspersed by plantations and areas of dense short bamboo brush. The territory bordered on the Belize River (see map p. 153), and various local informants commented on the howlers crossing the strong flowing river to the other side to forage. The howlers also had to jump across wide gaps in the vegetation or descend to the ground to get to certain feeding areas. Dogs were often present, and several months earlier a juvenile female howler was killed by a dog when the group was crossing on the ground.

Some activity patterns in this group differed from those seen in other groups. This group, for example, started to move and forage before 5:30 AM. At this time the small infants (I_1 and I_2) were locomoting on their own while the adults were feeding. In all other groups

the small infants clung to their mothers during the cool morning hours.

Interactions with the mother

Contact between mother and infant was less frequent and of shorter duration in this group than was true for the 4 months old infant in group I (and, of course, the tiny infant in group III) (tables 5 and 6). The mother in group VI was very permissive toward her MI_1 , and mother-infant interactions were well coordinated. Clinging was the most frequent behavior within this dyad, followed by affiliative and play interactions (tables 15, 16). The infant sometimes clung to its mother with only one limb, and was seen pulling itself up to its mother by her fur. This acrobatic feat was at one time followed by a peculiar posture where the infant rested on the mother's back with its arms crossed behind its head, looking up in the sky. It remained in this position for over 6 minutes. None of the other infants were ever seen in this type of a position, which was only once observed in an adult male.

The affiliative bond between mother and infant was strong; the infant was frequently sitting very close to the mother, muzzling intermittently. Play consisted mainly of the infant manipulating parts of the mother's body and jumping on her back in an exuberant manner.

Interactions with the adult male

Although the MI_1 did approach the adult male for affiliative and play interactions, the adult male seldom responded. This behavior contrasts with that seen in other groups where the adult males frequently responded to approaches by the infants. In this group agonistic interactions occurred which were never witnessed in any of the other howler groups studied. On two different occasions the adult male slapped

the MI_1 and the MI_2 as they were jumping together on his back for a short while. Apart from these instances, however, the adult male either tolerated the infant walking over or jumping on him, or he got up and left. The adult male in group VI seemed to be more irritable than any of the males in the other groups. Perhaps the precarious environment - wide gaps, barking dogs, river crossings - had an impact on his disposition.

Interactions with females

The females (AF , FJ_2 , FJ_1) in this group congregated frequently, a situation which facilitated interactions with the infant. No clinging interactions were witnessed between the MI_1 and females other than the mother. Affinitive and play interactions, however, were numerous (tables 15, 16). Most of the contacts were initiated by the infant. A great range of affinitive interactions occurred - huddling, hugging, muzzling, and touching. Play related mostly to the exploratory type, although short playchases took place between the FJ_1 and the small infant. All of the females were tolerant of the infant at all times. Alloparenting by females did occur while the mother went off to feed; however, it was observed less frequently than in group I.

Interactions with the male infant₂

Play interactions between these two infants were almost exclusively of the rough-and-tumble type. They very much resembled those seen between the two infants in group I, where wrestling, pulling of arms, legs, and tail, holding heads, and playbiting was prominent. These infants played less frequently than the infants in group I; the playbouts, however, lasted on the average roughly twice as long. I presume that the MI_1 in this group did not need its mother for arousal-

decreasing contact between play bouts as often as the MI₁ in group I.

Interactions with the physical environment

The MI₁ interacted considerably more frequently and for longer periods of time with the physical environment than the other infants of this age class. Locomotor activities were predominant over manipulatory exploration of the vegetation.

General tendencies of parental behavior in group VI

Parental behavior within this group was very puzzling indeed. It is surprising to see such a young infant spending more than a quarter of each day (27.4 % of the observation time) away from group members. It is not less astonishing to see an infant of that age locomoting on its own during cool morning hours when other infants of age class I and even older infants clung tightly to their mothers for warmth. One incident, however, was more surprising still. The incident occurred as follows:

Feb. 11, 3:03 PM: Group VI came from the forested area to a more open region which intergraded into a plantation. In order to avoid descending to the ground, the animals had to arrive via a tall tree overlooking a wide gap. The adult male was the first to make the spectacular jump from a high tree on the embankment, approximately 7 meters out and down onto a leafless tree. From there he climbed a higher tree from where he could overlook the whole area. He started to howl loudly, facing the group on the other side pacing back and forth. The two infants were locomoting alone in the vegetation with the rest of the group on the other side. As the mother of the MI₁ ducked down to jump, the MI₁ climbed on her back. It was holding onto a branchlet above itself with one hand and had not yet grabbed the mother's fur when she jumped. The small infant was lifted off the mother's body, swinging up into the air still clinging to the branchlet above it. When the FJ₂ prepared to jump, the small infant hurried on her back² and made it safely to a branch on the lower tree which swung out enormously when hit by the weight of the animals. The mother of the MI₂ jumped next without her infant followed by the FJ₁. The MI₂ was left alone on the high tree, moving back and forth nervously, then he jumped. Since there was

no foliage on the tree below, it was difficult for the infant to grab a hold of a branch with its tiny hands. It did succeed, however, and walked up to where the group was waiting. The adult male stopped howling only when the last group member was safely on the other side.

The whole group seemed very nervous at this jump (including the observer).

It is surprising that at a gap of this size the mothers did not protect their infants. At smaller gaps the infants were usually seen clinging to their mothers or locomoting between the adults. Whether the danger factor, or the high concentration necessary to make the jump, made the adults forgetful of their infants, is not clear. Perhaps a jump of this kind even with a small infant would make it still more hazardous. As mentioned previously, 6 months earlier a FJ_1 was killed by a dog when the group was crossing on the ground to get to the same feeding area the group was heading for now. Possibly this incident led the howlers to prefer jumping the gap. The Baldwins (1973) observed that at gaps mothers usually waited for their infants or, at least, slowed down for the infant to catch up. In one case, however, a mother jumped a gap, leaving her infant behind with other group members. The infant finally dared to jump 10 meters into a vine-matted thicket. It could not be ascertained whether the infant survived the jump.

Summary - Infants of Age Class I

The above discussion has shown a range of parental/infant behavior patterns within age class I.

The pattern of interactions of the MI_1 in group III, which is characterized by a close mother-infant bond, stands in contrast with that of the MI_1 in group VI, which is marked by much less contact with the mother combined with a greater tendency to interact with the

physical environment. Considerable differences in the patterns of interactions are also apparent between the MI_1 in groups I and VI, which are close in age.

With respect to adult male-infant interactions, we find close contact and some active participation on the part of the adult males in group I and to some extent in group III, while in group VI the adult male, although tolerant to repeated approaches by the MI_1 , rarely actively participated in interactions and on two occasions showed agonistic behavior toward the MI_1 .

All three infants of age class I passed roughly the same amount of time interacting with a peer. There is a great difference, however, in the frequency with which peers interacted, resulting in many short interactions in group III, fewer but longer interactions in group I, and little more than half as many interactions in group VI (as compared to group I), which, however, lasted about twice as long as those in group I. The length of the playbouts between peers is held to reflect an infant's degree of independence from its mother. It was puzzling to see that mothers of very young, still rather uncoordinated infants, allowed them to participate in play to the same extent as older infants.

Alloparenting occurred in all three groups, with different animals taking care of the infants. In group III the MI_3 took care of the small MI_1 , in group I both the adult female and at times the adult males shared in infant care in the absence of the mother, whereas in group VI only the females engaged in alloparenting.

Permissiveness toward the infants was exhibited in all groups by all group members. In group VI, however, this behavior was so pronounced that the small infant was sometimes placed in jeopardy, as was

seen in the crossing of the wide gap. Whether and to what degree these caretaking patterns may be adaptive, will be further highlighted in the conclusions.

2. Infants of Age Class II

Female Infant₂ - Group I

Group I consisted of 2 AMs, 2 AFs, 1 FI₂, and 1 MI₁. Its small territory of only 700 m² was adjacent to the Belize River and surrounded on three sides by pastureland (see map p. 153). For further description see MI₁, group I, p. 44).

Interactions with the mother

Despite the infant's very good coordination, which was most evident in arboreal gymnastics and above all during rough-and-tumble play with the MI₁, this infant shared one third of all interactions with its mother and spent more than half the day in close physical contact with her (tables 7, 8). In agreement with the Baldwins (1973) observations on early mother-infant coordination, this infant still closely responded to the mother's activities, and it was up to the infant to catch a ride during troop progressions, although the mother was sometimes seen to slow down and wait for the infant. At this stage, the infant still depended on the mother to cross large branches, where it tended to slip. Where the vegetation allowed (small branchlets, no gaps, etc.), however, this infant moved at distances of up to 15 meters away from the mother. Infant and mother were frequently seen huddling together and touching one another, and gentle play activities were common (playing with parts of the body, pulling of tails). The mother was always very permissive, and never retaliated when the infant jumped

on her or took leaves out of her hands to nibble on or to throw away.

Interactions with the adult males

In this group the two adult males could not always be recognized individually, and for this reason the data on these two animals were lumped.

The males frequently engaged in interactions with the FI₂. At various times a male was seen pulling the FI₂ to his chest, hugging it. The infant then climbed on his head, holding on to his chin, or it climbed all over his body. One sequence of affiliative interactions took place as follows:

Jan. 25, 6:20 PM: The adults had settled down for the night in close vicinity. The FI₂ was resting ventrally with its mother. All of a sudden it hurried away from its mother toward the adult male, who was sitting at a distance of 1.5 meters. The male opened his arms and held the infant, muzzling it occasionally. The infant remained with the male for 7.3 minutes, then returned to the mother clinging ventrally for the night.

The adult males took care of the infant when the mother was foraging; the infant was never seen to sleep with the adult males.

Interactions with the adult female

Although actual physical contact between the FI₂ and the AF in this group was low (tables 7, 8), the FI₂ often found itself in the vicinity of this female while playing with her MI₁. Huddling and occasional muzzling was observed between the FI₂ and the adult female, which was as tolerant of this infant as of her own. Alloparenting behavior on the part of the adult female was frequently seen.

Interactions with the MI₁

Peer interactions consisted almost exclusively of play (tables 17, 18). The FI₂ was well coordinated, and was able to play for long

periods of time with the MI_1 , which returned to its mother more frequently for contact before resuming play interactions. Interference with the vigorous play activities by adults was never witnessed. (For further detail on play interactions, see p.48, Interactions with the female infant₂).

Interactions with the physical environment

The FI_2 interacted less frequently and for a shorter period of time with the physical environment than the other two infants of this age class (tables 7, 8). Locomoting through the vegetation and engaging in arboreal gymnastics predominated over the manipulation of vegetal matter. The mother never restrained the infant when it wandered off exploring the environment, and the infant always returned at its own initiative.

Male Infant₂ - group V

Group V was composed of 4 animals: 1 AM, 1 AF, 1 FJ_2 , and 1 MI_2 . The territory of this group consisted of undisturbed forest adjacent to the Belize river (see map, p. 153).

Interactions with the mother

At the approach of the observer, the mother jumped 3 to 4 meters down from a higher tree to join her infant. Physical contact between mother and infant did not, however, occur at this time. The infant continued to locomote in the vegetation and to engage in arboreal gymnastics. Mother-infant interactions were more frequent than in the other two groups with infants of age class II, but were of shorter duration than in group I. The mother was seen at times to push the infant on her back with one hand; generally, however, it was left to the

infant to catch up with the mother to hitch a ride.

Most of the mother-infant interactions were of the affiliative type (table 19) predominantly touching, but hugging, huddling, and muzzling was also observed. The following sequence was recorded:

Feb. 9, 1:25 PM: The mother touched the infant's head with her right hand first, then with her left hand. She pulled the infant close to her, passing with her hands through its fur several times, spreading it somewhat. After this gesture, which resembled a grooming bout, the mother held the infant's head, muzzling him.

Play interactions were largely due to the infant's initiation, and consisted mainly of playful investigation of the mother's body, especially the tail. Despite the infant's young age, it was sometimes seen to locomote independently from the mother - although very close to her - during short troop progressions.

Interactions with the adult male

The proportion of male-infant interactions in the behavioral profile of this infant was second to the FI₂ in group I regarding frequency, and was greater in duration than in the other two infants of this age class (tables 7, 8). Interactions within this dyad were primarily of the affiliative kind - touching, muzzling, and huddling. The infant was seen twice to sit close to the male with his back touching the male's ventrum. The male held the infant with one hand. It looked as though the infant was sitting in his lap. Play interactions were almost exclusively initiated by the infant, which was frequently observed to climb across the male's back, jumping on it, or investigating a part of his body. Once the infant was seen hanging from the male's tail. The male tolerated this type of acrobatics, but was, on other occasions, observed to leave the scene when the infant became too rambunctious. Signs of aggression, however, were never seen.

Interactions with the female juvenile₂

Female-infant interactions were slightly more pronounced in this group than in group I, and less than in group VI (tables 7, 8). Most of the interactions within this dyad were of the affiliative type - hugging, muzzling, touching - followed by play interactions. The infant was observed various times to play actively with the FJ₂. Both animals were hanging from their tails swinging, while pawing at one another; sometimes the FJ₂ pulled the MI₂ down into the lower part of the vegetation. Once a play chase was witnessed, with the FJ₂ chasing the infant through the vegetation. The large FJ₂ was very active - more than other late juveniles. She leapt at high speeds through the vegetation and often disappeared for extended periods of time. The liveliness of this juvenile may have accounted for the active play bouts between this animal and the MI₂. During play with the MI₂, the FJ₂ seemed to restrain herself. This type of play is common in other species of non-human primates, for example Barbary macaques (Macaca sylvana), where older animals do not fully use their strength when playing with a younger individual (Burton, 1972).

Interactions with the physical environment

The MI₂ interacted more frequently with its physical environment than with its mother (table 7), and spent almost as much time in the environment as with its mother (table 8). Interactions with the physical environment included locomotor play, arboreal gymnastics, and manipulative play. Sometimes the infant would swing wildly by its tail while manipulating leaflets and branchlets. The infant was seen dropping down into the vegetation, catching itself by its tail. Jumps of 3 meters into the foliage were commonplace. This infant was the most

accomplished acrobat of all infants observed. Its manipulative play was more reminiscent of that of infants of age class III than of its own age class. It pulled and pushed lianas in all directions, and twisted leaves by the stem, nibbling intermittently, then watched them swirl down. The absence of a peer in this group may have been the reason for this infant to engage in a great variety of manipulatory activities.

Male infant₂ - Group VI

Group VI was composed of 7 animals: 1 AM, 2 AFs, 1 FJ₂, 1 FJ₁, 1 MI₂, and 1 MI₁. This group ranged through high jungle area, interspersed by plantations and areas of dense short bamboo brush. The territory bordered on the Belize River (see map p. 153). (For further group description and group habits, see MI₁, group VI, p.50).

Interactions with the mother

Although the mother's permissiveness was also very prominent in this dyad, the mother was observed to move away when the MI₂ sat in close body contact with her, and once she tried gently to pull the infant off her back. She did not succeed and subsequently left him sitting there. Otherwise mother-infant interactions were well coordinated. Within this dyad, affiliative interactions - mainly huddling and touching - were more frequent than clinging and play, while clinging interactions lasted longest (tables 21, 22). During play interactions the MI₂ was seen to approach the mother, who either ignored it or played with it gently, pawing at the infant which, in turn, pawed back at the mother.

The gentle affiliative and play behavior between mother and

infant stands in contrast to certain other behaviors. The MI_2 was observed to locomote on its own through the vegetation during the cool morning hours while the adults were foraging. Other infants of this age class clung to their mothers till it warmed up. The mother's behavior at the wide gap (see p. 53-54 for description) was especially surprising and will be further considered in the Conclusions.

Interactions with the adult male

Although interactions between this infant and the adult male in this group were almost as frequent as in groups I and V (table 7), their duration was very short (table 8). The infant was frequently seen to approach the male, walking across his back, touching and muzzling him. Sometimes the male did not respond, at other times he got up and moved on to a different place. The infant was seen to pursue the adult male in a persistent manner, causing him to get up and move away several times in a row. Normally the male showed his unwillingness to interact with the infant by escaping from his resting place, but twice the male slapped the MI_2 when it was jumping on his back together with the MI_1 . The adult male in this group was considerably less inclined to play with the infant than the males in the other groups with infants of age class II. The stressful environment under which this group lived could be responsible for his disposition.

Interactions with females

All three females (1 AF, 1 FJ_2 , 1 FJ_1) in this group were very tolerant of this infant's approaches. Interactions with the adult female and the FJ_1 were characterized by play interactions - the infant was usually playing with parts of the adult female's body - while it mainly played rough-and-tumble with the FJ_1 . Interactions with the FJ_2 were

characterized by affiliative behavior (table 21, 22). The FJ_2 often responded to the initiations of the MI_2 by touching or muzzling the infant, or - at times - by moving away. The MI_2 freely interacted with the females as well when the mother left to forage.

Interactions with the MI_1

Peer interactions were characterized by an overwhelming proportion of play (tables 21, 22). Play was vigorous, mostly of the rough-and-tumble type and very much resembled the play seen between the FI_2 and the MI_1 in group VI. The infants hung by their tails, pawing at one another, pulling, pushing, and playbiting.

Interactions with the physical environment

Non-social interactions were frequent and of long duration. The MI_2 in this group engaged in this type of interactions almost to the same extent as the MI_2 in group V. In this infant, however, arboreal gymnastics were more pronounced than manipulatory play. Very similar to the MI_2 in group V, this infant hung from its tail, twirling around while playing with sticks and leaves. It sometimes let go with its tail, dropping into the foliage two to three meters below. As was true for the other infants observed, neither the mother nor the other group members were ever seen to restrict the infant from wandering off or interfered in any way with its activities.

Summary - Infants of Age Class II

Contrary to the general trend toward individual variability among infants, there is no statistically significant difference in the frequency of interactions between the individual behavioral profiles of the infants₂ of groups V and VI. Table 7 indicates a

close agreement in the frequency of mother-infant and male-infant interactions as well as the interactions with the physical environment. This result is surprising, since both group composition and the habitat of the two groups differed greatly. A close agreement in the duration of interactions would also be necessary, however, in order to initiate conclusions as to why the patterns of interactions in these two groups should not differ. The results have shown, however, that the agreement in the frequency of interactions was accompanied not only by a difference in total duration but the proportions of the types of interactions varied as well (tables 7, 8, 19-22).

Considering both quantitative and qualitative data, inter-individual variability among infants of age class II was as pronounced as it was among infants of age class I. Apart from general characteristics such as the permissive attitude in parental caretaking strategies extended to infants by all group members, certain differences emerged. Although generally tolerant to the infant's approaches, the mother in group VI was observed several times to move away from her MI_2 as it sat down close beside her. At one time she even tried to pull the infant from her back. Behavior of this type was not witnessed in other groups with infants₂, and, apart from group II where the mother had been seen to move away from her FI_3 , these open signs of rejection were not observed among any mother-infant dyad. Even the large infants of age class III were permitted to sit on their mothers' backs.

Male care of the three infants of age class II differed primarily in a qualitative way. While the adult males in groups I and V were observed to participate actively in infant care, the adult male in group VI, although generally tolerant toward the infant, sometimes

showed his unwillingness to interact with the infant by moving away as soon as, or shortly after the infant had made physical contact, and - on two occasions - by showing aggression. The MI_2 in group VI was seen persistently to follow the male, who subsequently changed places several times in a row. This adult male in group VI seemed to be protective of the group as a whole - as observed in the crossing of the wide gap - but he was little inclined to get involved in infant care. As was mentioned earlier, the stressful environment could have contributed to his disposition.

Among the three infants of age class II, the male infants in groups V and VI passed considerably more time interacting with the physical environment than did the FI_2 in group I. Regarding the two male infants in groups V and VI, manipulative play was much more prominent in the male infant in group V. This type of behavior, which has not been observed to occur much in other howler species (Baldwin and Baldwin, 1973; Neville, 1972), was also expressed in infants of age class III (groups II and III). The pattern that emerged regarding manipulative play relates to group size. In each of the groups II, III, and V where the manipulation of the vegetation was prominent, only four group members were present, and possibilities to interact socially were thus restricted; this condition could lead an infant to engage more often and for longer periods of time in manipulative play. In the three other Belize groups - I, IV, and VI - which consisted of at least six animals, this habit was much less prominent.

As was already mentioned in the first section of the discussion on the Individual, parental caretaking in group VI - despite the permissive element which was common to all groups - differed in several

ways from parental care in other groups. The MI_2 in group VI was observed to locomote on its own in the early morning hours - before 0600 - when it was still rather cool. This behavior was not seen in any other group in Belize, and reports by Baldwin (1973) refer to the close physical contact between infant and mother during cool temperatures. Incidents of this type, as well as an infant's extended non-social periods of interactions and exceedingly permissive parental behavior, are trends which suggest fostering of independence in the young infants by the adults.

3. Infants of Age Class III

Female Infant₃ - Group II

Group II was composed of 4 animals: 1 AM, 1 AF, 1 FJ_2 and 1 FI_3 . The group's range was restricted to a narrow strip of gallery forest between the Belize River on one side and a mud-road with adjacent grazing land on the other (see map p. 153). Local observers reported that the group sometimes swam across the river in search of food on the other bank. During the present study the group was never observed leaving the described home range. Despite the fact that access into this area was made difficult due to the steep and muddy banks of the Belize river, this group appeared to be more retiring than any other at the approach of the observer. During disturbances howling was frequent and of long duration. Group cohesion was less marked than in most other groups observed. The adult male generally sat by himself higher in the vegetation, with other group members at a distance of up to 15 meters. Frequent howling by the adult male supports the idea that he may have used the higher position in the trees for observation and

thus as a protective technique. The FJ_2 was seen to leave the group for short periods of time, to reappear later.

Interactions with the mother

Mother and infant slept together in close physical contact, often huddling against one another. During resting periods, the infant was sometimes sitting close to the mother, but was also observed resting by itself at distances between 1 and 15 meters from her. Twice the infant sat on the mother's back, clinging to her fur. The mother tolerated the large infant in this position. Several times the infant was seen sitting beside the mother with its tail wrapped around her body. When the infant was in physical contact with the mother, it had a habit of gently poking its head into her stomach; the mother then put her arm around the infant. This type of affiliative interaction between mother and infant was frequent, and comprised a high proportion of mother-infant interactions (table 23). While the mother usually responded with affection to the approaches of her infant, she sometimes got up and left after the infant had been sitting in close contact with her for a short while. It may be conjectured that the mother wanted to discourage too many close interactions with the FI_3 in order to further the infant's independence.

Interactions with the adult male

The FI_3 and the adult male associated rarely and only for short periods of time (tables 23, 24). All interactions were of the affiliative type. Once the adult male was seen gently touching the infant's head, and three times the infant was observed sitting in close physical contact with the adult male. One morning the male approached the infant on several occasions. Each time the infant moved away

before the male came in body contact. Whether the male wanted to associate with the infant, or tried to supplant it by showing his authority, could not be determined. Contact between the male and the FI_3 was too infrequent to determine the kind of relationship that prevailed between these two animals. Since a much closer bond had developed between the adult males and the male infants of age class III (groups III and IV) than between the adult male and the female infant in this group, it may be questioned whether at that stage of infancy male infants would associate more closely with adult males. The situation as it existed in group III in Tikal, however, contradicts this assumption. In the Tikal group the adult male was frequently seen to touch the FI_3 and to locomote with it in close body contact. The male was very protective of the infant at all times, especially when it was locomoting through the vegetation where a juvenile female spider monkey, which was traveling with the howler group, was frequently trying to take hold of the infant.

Interactions with the FJ_2

As was the case in the infant-male dyad, the relationship between the FI_3 and the FJ_2 was characterized by few interactions, a great proportion of which were of the affiliative type, the rest involving play (table 23). The infant and the FJ_2 were seen huddling close together, and only once during the time of observation did a short but vigorous play activity take place. During this interaction the animals hung by their tails, grappling with arms and legs, and then chased one another through the trees. Frequent activities, such as arboreal gymnastics and manipulation of the vegetation, demonstrated that the infant was interested in play. Possibly the FJ_2 was beyond

the play stage. During my observations on Alouatta seniculus in the Frankfurt Zoo, vigorous play interactions were frequent between a 10 months old FI₃ and a FJ₂ which was close to adulthood. The caged condition could possibly account for this increased willingness to play, or maybe the diet, which consisted of little leafy material, was a factor. Baldwin and Baldwin (1978) suggested that play decreases as a young howler becomes more dependent on plant food which demands energy for digestion. In Tikal vigorous and long-lasting play bouts were witnessed between younger animals, while late juveniles engaged little in play activities demanding physical exertion.

Interactions with the physical environment

The FI₃ in this group engaged in more interactions with the physical environment and passed more total time on its own than any of the other infants (tables 9, 10). Interactions with the environment consisted of arboreal gymnastics, during which the infant vigorously swung by its tail and limbs, intermittently jumping into the foliage. The FI₃ passed a great amount of time playing with the vegetation. Play explorations such as the following were frequent:

The infant was stretched out on a branch, pulling leaves toward its body, then letting them snap back through its fingers. The infant then suspended itself by its tail, pulling at the branchlets, intermittently nibbling on some leaves. It grasped a dry stick which it turned in all directions, looking at it intensely. It chewed at the upper end of the stick, then extended its arm holding the stick down before bringing it back up to its mouth. This procedure was repeated several times.

The large leaves of the trumpet tree were also used during exploratory play. The infant twisted the stem of the leaf in its hands, then let the rotating leaf glide through the air, following it to the ground with its eyes. Many large trumpet leaves left the tree in this fashion.

Male Infant₃ - group III

This group consisted of 4 animals: 1 AM, 1 AF, 1 MI₃, and 1 MI₁. The home range, which extended several kilometers west from the banks of the Belize River, was covered with relatively undisturbed high forest (see map p. 153). Other howler groups ranged close to this area, none, however, contained infants.

Interactions with the mother

Although the MI₃ foraged independently from its mother - even crossing gaps on its own - it was twice seen sitting on its mother's back clinging to her tightly while she rested. The mother tolerated the large infant in this position, even though her tiny MI₁ clung to her ventrally.

Apart from one play interaction, the relationship between the MI₃ and its mother was characterized by affiliative behavior (tables 25, 26). Huddling together was the most frequent affiliative interaction within this dyad, and the mother was rarely seen to move away from the MI₃. Whether the MI₃ huddled close to its mother for the sake of being with her or to be close to the small MI₁, could not be determined.

Despite the affiliative relationship between the infant and its mother, it was left unattended during group progression where wide gaps had to be crossed. One particular crossing could only be achieved in the following manner:

The mother (her small MI₁ clinging ventrally) swung back and forth on a thin flexible tree. As the tree swung out close to the vegetation on the other side of the gap, the mother extended her body far out, grabbing a branch with her arms, while she released her feet and tail from the swinging tree. The adult male followed in the same manner. The MI₃ hesitated at the

gap for an instant, then turned around to make a detour in order to catch up with the adults.

The infant was not strong and heavy enough to make the tree swing far enough out to reach the other side. Whether the adults could have crossed the gap with the MI_3 clinging dorsally, could not be ascertained.

Interactions with the adult male

Apart from a single play interaction, the relationship between the MI_3 and the adult male was characterized by affiliative behavior (tables 25 and 26). The MI_3 was observed resting and sleeping while huddling close to the male at a distance of 12 or more meters from the mother. Although interactions between the MI_3 and the adult male were not very frequent, they were of long duration (mean length 52 minutes; tables 9, 10). Of all the infants observed, only this one was seen sleeping with the male at a distance from the mother. It is possible that the mother's preoccupation with the small MI_1 led to prolonged associations between the MI_3 and the adult male. Male-infant interactions were longer, while mother-infant interactions were more frequent (tables 9, 10). During group progressions, the MI_3 followed the adult male closely, foraging at short distances from him.

Interactions with the MI_1

Interactions between the MI_3 and the MI_1 were frequent but of short duration (tables 9, 10). Whenever the mother and the MI_3 came into close physical contact, the MI_1 transferred from the mother's back or ventrum to the infant's back. Although there was some affiliative behavior - hugging and muzzling - between the two infants, simple play activities predominated (tables 25, 26). The MI_1 initiated most play interactions, playing in an exploratory manner with the MI_3 's

hair, ears, and tail. The MI_1 scooted around the MI_3 's back, grabbing its fur when it started to slide off. The MI_3 endured the small infant's approaches without retaliation, and permitted the tiny infant to explore the vegetation without ever restraining it. During investigations of the close environment, the MI_1 never completely left the older infant's back. Sometimes it stood in the vegetation manipulating leaves, while clinging with only one foot to the MI_3 . Due to the age difference among the two infants (MI_3 was 12 months old, MI_1 was 2 months old) and the fact that the MI_1 was not yet capable of engaging in two-way play activities, the MI_3 was taking care of the MI_1 rather than playing with him. One incident indicated that in this respect the MI_3 was very much needed:

Feb. 3, 1:27 PM: The adult male started to howl loudly. The mother who was foraging with the MI_1 riding ventrally, hurried close to the MI_3 . As she lowered her body, the MI_1 immediately transferred onto the MI_3 's back. The mother took off fast to join the male in his howling. Following the intensive howling concert - it lasted roughly 8 minutes - the mother hurried back to the infants. The MI_1 returned to the mother's back and she continued foraging.

Whether in the case described above the mother would have been able to howl with the infant clinging ventrally, could not be determined, but during intensive howling the body of the monkey shakes and vibrates intensively. Alloparenting in Alouatta palliata pigra will be further discussed in the section on the species.

Interactions with the physical environment

The infant spent a higher proportion of interactions with the physical environment than with any one group member (tables 9, 10). It engaged in arboreal gymnastics which were vigorous and carried out in rapid succession. The infant swung by its tail and limbs, jumping

onto branches and into the foliage. Manipulation of the vegetation was observed frequently. The MI_3 often hung by its tail alone, pulling leaves and branchlets toward him, then letting them snap out. This infant had a preference for the large leaves of the trumpet tree, which it manipulated in the same fashion as the FI_3 in group II.

Male Infant₃ - Group IV

Group IV was composed of a total of six animals: 1 AM, 1 AF, 1 MJ_2 , 2 FJ_2 and 1 MI_3 . The group was generally encountered in an area where plantations grade into bamboo brush and dry forest as well as on the adjacent tall fig trees along the Belize River. Group IV was characterized by great coherence, with animals congregating closely together during rest periods. Many affiliative interactions were witnessed in this group, not only between the infant and other group members, but also among adults and juveniles. The adult male was repeatedly observed scooting toward the adult female, touching her fur, muzzling, and huddling. The adult female was observed grappling through the male's beard for several minutes at a time. No agonistic interactions of any kind were ever witnessed within this group.

When moving across a gap in the canopy, down a liana or between trees, the infant was always closely preceded and followed by other group members. When foraging, the group sometimes dispersed over a considerable distance of up to 50 meters. The infant was always in close vicinity of a group member, generally the mother, the adult male, or the MJ_2 . During times of potential danger - such as a dog barking or a bird shrieking - the MI_3 hurried close to a group member, jumping on his or her back or shoulders. All group members tolerated the

large infant sitting on them.

Interactions with the mother

Mother and infant slept in close physical contact and spent most of the resting periods together, often joined by other group members, but were frequently observed to forage at a distance. The mother-infant dyad was characterized by a great amount of affiliative interactions (tables 27, 28). Sequences similar to the following were frequently observed:

The mother was touching the infant's head, pulling it toward hers, nuzzling it. The infant proceeded to take the mother's head between its hands, nuzzling her nose. The mother continued gently touching the infant's head several times, stroking it softly while putting an arm around its back, hugging the infant.

Play interactions were entertaining and amusing. At one occasion the infant bobbed back and forth playfully running between the mother and the adult male, touching first one and then the other. Mother and infant then rested on a branch with arms and legs dangling while the infant continued playing with the mother's tail. Play interactions were characterized by more bouncy movements than affiliative interactions.

Interactions with the adult male

The interactions between the adult male and the infant were also characterized by affiliative behavior (tables 27, 28). The male was often seen to touch and hug the infant, pulling it towards his body, putting his arm around it. Once the male was seen to groom the infant. The grooming lasted 4.6 minutes, during which time the male parted the infant's fur with both hands, licking it. It appeared that the infant had a botfly infestation or small wound. Whether the male was trying to cleanse this sore spot or was just grooming, could not be ascertained. It is notable that grooming was rarely observed within these groups.

During 477 hours of observation, only 4 short grooming bouts were witnessed. Carpenter (1934) and Bernstein (1964) also commented on the rarity of this behavior, while Neville (1972a) observed considerably more grooming behavior in Alouatta seniculus. Among a small group of Alouatta seniculus in the Frankfurt Zoo, grooming was frequent, amounting to 23.9 % of the total number of interactions. Whether the caged condition was responsible for this high frequency or whether grooming in Alouatta seniculus is more prominent than in other species, is not clear.

The MI_3 was seen jumping onto the adult male's back, clinging to him. Play interactions were initiated by the infant, which characteristically bobbed back and forth, climbing across the male's back several times. The male sometimes held the infant's leg or tail, or playfully pushed against it.

Apart from interactions involving close physical contact between the adult male and the MI_3 , the infant was frequently seen foraging close to the male or sitting at a short distance from him. This type of close association, although not in physical contact, may very well indicate the infant's intent to observe the adult male and behave in reference to him as suggested by Carpenter (1965).

Interactions with the male juvenile₂

Contact between the MI_3 and the MJ_2 was usually of the affiliative type (tables 27, 28). These animals were frequently huddling together. Once the MJ_2 pulled himself up by a branch, touching the head of the MI_3 with both hands. The MI_3 then climbed across the back of the MJ_2 , pulling its hand through his fur. Play activities between these two animals were more vigorous than those between this infant and the adult male; they were marked by jerky, bouncy movements, pulling

of tails and limbs. One of the play activities was probably directed at the observer:

Feb. 13, 1:48 PM: The MJ₂ was bouncing on a branch above the observer dropping down small sticks. One of the FJ₂s ran to another branch, somewhat closer to the observer. The MI₃ jumped on an even closer branch. Then the MJ₂ took his turn coming closer. Finally the MI₃ jumped on the branch closest to the observer, at a distance of about 2.5 meters.

This play activity resembled some kind of daring game or perhaps a territorial display. The observer did not seem to represent any kind of danger since during dangerous situations - for example, dogs barking - the MI₃ associated closely with other group members.

Interactions with the female juveniles₂

Interactions between the MI₃ and the two female juveniles were lumped, since these animals could not be recognized individually. The MI₃ interacted less with each of the FJ₂s than with the MJ₂. Interactions between the MI₃ and the two FJ₂s were of the affiliative type, huddling was observed most frequently. One of the FJ₂s was seen pulling the infant, who was sitting on a lower branch, up toward her. The two animals were holding each other's heads in their hands, muzzling and playfully bouncing back and forth.

Interactions with the physical environment

Interactions with the physical environment were not as frequent and long lasting in the MI₃ of this group as they were among infants of age class III in groups II and III (tables 9, 10). Arboreal gymnastics were most pronounced. The infant was frequently seen hanging by its limbs - either its tail and legs, its tail and one arm, one arm and one leg, or by its tail alone - while swinging and manipulating leaves and branchlets.

Summary - Infants of Age Class III

A great range of behavior patterns existed among the three infants of age class III. Although a trend toward reduced mother-infant contact is apparent among all three infants of this age class, variation still persisted in frequency, duration, and, especially, the types of interactions. Thus, for example, in the mother-infant dyad in group II, no play occurred, while in group IV, 14.3 % of all mother-infant contacts involved play. Affinitive mother-infant interactions also varied greatly among the three infants (tables 23 to 28).

Patterns of association among infants and males differed considerably, ranging in duration from 2.8 % in group II to 49.1 % in group III (tables 24, 26). The males in group IV most actively engaged in interactions with the MI_3 , while in group III, the prolonged contact between the MI_3 and the adult male was of a more passive sort (e.g., sleeping and resting together). The high male-infant contact for frequency (group IV) and duration (group III) of interactions, stands in contrast to little male-infant contact in group II (tables 23 to 28). Considerable differences in the 'bonds' which developed between infants and group members other than the mother and males could be ascribed to the difference in group membership among the groups under investigation.

Patterns of interactions with the physical environment indicated that the FI_2 in group II interacted more frequently and for longer periods of time in a non-social manner than did either of the male infants in groups III and IV. Patterns of interactions with the physical environment were very similar in the infants of groups II and III. Both infants passed much time manipulating the vegetation in

precisely the same manner (twisting and turning leaves and sticks, intermittently nibbling on them, etc.). The MI_3 in group IV, on the other hand, engaged less in manipulative behavior.

Individual variability was still very strongly pronounced in infants of age class III.

The above discussion on each howler infant has shown that variability in patterns of parental behavior may express itself in many different ways. The question arises: how does this great individual variability seen in the patterns of interactions among infants of different groups allow us to detect unifying trends? In the following section, modal tendencies as they existed within three separate age classes of howler monkeys are presented with the intent to show an average progression in the patterns of parental behavior in the course of a howler's infancy.

CHAPTER FIVE

THE AGE CLASS

RESULTS

The interactions are summarized for the three infants of each age class. Thus, for example, table 29 shows that the three infants of age class I were involved in a total of 1282 interactions, of which 556 took place between the infants and their mothers, 410 between infants and group members other than mothers, and 316 were directed to the physical environment. The resulting proportions provide the average participation of an infant of age class I. Tables 29 and 30 (figures 1 and 2) illustrate the proportions of both the frequency and the duration of interactions for all three age classes.

The data are examined relative to the question of change in parental behavior patterns with age of an infant. Emphasis is placed on the following issues:

1. Interactions between infant and mother;
2. Interactions between infant and group members other than the mother ('others');
3. An infant's interactions with its physical environment.

1. Interactions between infant and mother

The initial frequent and long lasting contacts between mother and infant declined steadily with age of an infant (tables 29, 30, figures 1, 2). The proportions in both frequency and duration of mother-infant interactions decreased from 43.4 % (age class I) to 34.0 % (age class II) to 27.2 % (age class III). The duration of mother-infant interactions decreased from 72.3 % (age class I) to 58.8 % (age class

II) to 28.1 % (age class III). To determine whether the change in mother-infant interactions between age classes is statistically significant, the following null hypothesis was proposed:

There is no significant difference between age classes in the frequency and duration of mother-infant interactions.

χ^2 one sample tests ($\alpha = .05$, $df = 1$) show that the observed differences are statistically significant between age class I and II ($\chi^2 = 20.93$, $p < 0.001$ for frequency; $\chi^2 = 13.65$, $p < 0.001$ for duration), and between age class II and III ($\chi^2 = 17.22$, $p < 0.001$ for frequency; $\chi^2 = 21.45$, $p < 0.001$ for duration). On these grounds the null hypothesis was rejected in all cases. Interactions between mother and infant thus decreased significantly in frequency and duration with age of the infant.

2. Interactions between infant and 'others'

In this analysis, group members other than the mother are not analyzed with reference to age-sex categories, but are treated as one single category. Table 29 indicates that contrary to the trends seen in the mother-infant relationship, where significant changes were apparent between age classes, we find very little change in the proportion of interactions between an infant of a particular age class and group members other than the mother. Proportions relating to the frequency of interactions range from 32.0 % (age class I) to 32.3 % (age class II) to 31.2 % (age class III) (figure 1). The picture looks somewhat different with regard to the duration of interactions between the infant of an age class and other group members. There is little difference between age class I (15.0 %) and age class II (14.5 %); the proportion of interactions in age class III, however, is higher (25.4 %, figure 2). To determine whether and where we are dealing with a

statistically significant difference between age classes, the following null hypothesis was tested:

There is no significant difference among age classes in the frequency and duration of interactions between an infant and group members other than the mother.

The χ^2 one sample test ($\alpha = .05$, $df = 1$) did not yield significant differences between age class I and II ($\chi^2 = 0.0912$, $p > .70$ for frequency; $\chi^2 = 2.03$, $p > .10$ for duration). Regarding interactions between age class II and III, no significant difference was obtained in frequency ($\chi^2 = 0.1918$, $p > .50$). In duration, however, the difference between age class II and III was statistically significant ($\chi^2 = 6$, $p < .01$). The null hypothesis was rejected for the difference in the duration of interactions between age class II and III; it was accepted for all other cases. Thus, there is little change in the frequency and duration of interactions between an infant and group members other than the mother throughout infancy, with the exception of an infant of age class III which spends on the average more time with 'others'.

3. Interactions with the physical environment

An inverse relationship to the steady decrease in mother-infant interactions can be seen in the steady increase in an infant's interactions with its physical environment. Table 29 (figure 1) shows that the frequency with which an infant oriented itself toward its physical environment increased from 24.6 % (age class I) to 33.7 % (age class II) to 41.6 % (age class III). The trend observed in the duration of non-social interactions roughly parallels that seen in frequency (table 30, figure 2). The time an infant spent interacting with the physical environment increased from 12.7 % (age class I) to

26.7 % (age class II) to 46.6 % (age class III). To test whether these differences are statistically significant, the following null hypothesis was proposed:

There is no significant difference among age classes in the frequency and duration of an infant's interactions with its physical environment.

The null hypothesis was rejected upon testing (χ^2 one sample tests, $\alpha = .05$, $df = 1$) for the difference between age class I and II ($\chi^2 = 22.78$, $p < .001$ for frequency; $\chi^2 = 15.52$, $p < .001$ for duration) and between age class II and III ($\chi^2 = 20.74$, $p < .001$ for frequency; $\chi^2 = 19.08$, $p < .001$ for duration). This result indicates that with age an infant directs progressively more of its attention to its physical environment.

4. Interactions with adult males

Given the above results on interactions between infants and group members other than the mother, the question arises as to what extent these findings correlate with the pattern of interactions between infants and adult males. In other words, is there a change in adult male-infant interactions with age of an infant?

Tables 31 and 32 (derived from tables 5 and 6 on the individual infants by means of summation of interactions of the three infants in each age class) show that the proportion of interactions between infants and adult males increased with an infant's age. Regarding frequency, the proportion of male-infant interactions increased from 8.6 % (age class I) to 12.1 % (age class II) to 17.6 % (age class III). The increase in the duration of interactions went from 2.1 % (age class I) to 3.6 % (age class II) to 16.1 % (age class III). These values indicate that interactions between males and infants not only occurred more frequently as the infants became older, but the interactions also lasted

longer (tables 31, 32). To test whether the difference between age classes are statistically significant, the following null hypothesis was proposed:

There is no significant difference among age classes regarding the frequency and duration of interactions between infants and males.

χ^2 one sample tests ($\alpha = .05$, $df = 1$) revealed statistically significant differences between age class I and II ($\chi^2 = 14.18$, $p < .001$ for frequency; $\chi^2 = 9.2$, $p < .01$ for duration) and age class II and III ($\chi^2 = 19.18$, $p < .001$ for frequency; $\chi^2 = 21$, $p < .001$ for duration). On these grounds the null hypothesis was rejected in all cases. This result indicates that male-infant interactions increase with age of the infant.

5. Trends toward peripheralization

In this study the assumption is made that group members that terminate interactions initiated by an infant, were to some degree reacting negatively to the interaction. Frequent terminations of interactions would eventually lead to the peripheralization of a group member. Table 33 - the values of which were obtained by computer tabulations of the initiator, receiver, and terminator of each interaction - exhibits the percentage of the total number of interactions which were terminated by either the mother, males, or other females. As indicated in table 33, the percentage of terminations is low, ranging from 3.7 % (age class I) to 3.6 % (age class II), to 5.2 % (age class III). To determine whether differences in the proportions of terminations of interactions are statistically significant, the following null hypothesis was tested:

There is no significant difference between the age classes in the proportion of interactions which were initiated by an infant and terminated by other group members.

(Other group members do not include infants). Statistical testing (χ^2 one sample tests, $\alpha = .05$, $df = 1$) revealed that the null hypothesis could not be rejected. There was no significant statistical difference regarding the terminations of interactions between age class I and II ($\chi^2 = 1.21$, $p > .20$) and between age class II and III ($\chi^2 = 3.14$, $p > .05$). This result signifies that the increase in the proportion of terminations of interactions is statistically not significant, although it does indicate a slight trend toward separation.

DISCUSSION

This discussion proceeds along the lines, which Mason (1973a) held to be of prime importance in the shaping of a well-adjusted animal, namely the initial close contact with the mother and a subsequent loosening of the bond as the infant matures. Changes with age of the infant are exemplified by considering interactions with its mother, group members other than the mother, the adult male, and interactions with its physical environment. Finally the discussion turns to the question of whether trends toward peripheralization - a common process especially among monogamous groups - are already noticeable in the older infant.

Orientation from the mother to the physical environment

A close bond between a mother and her young infant is found in most primate species. "The mother is the infant's ecological niche, its vital link with the future, and adjusting to that niche and making sure that the link is not broken, is the first developmental task that the infant must perform" (Mason 1973:20).

The second major developmental task which faces the infant is,

according to Mason, to prepare itself to function as an adult. "The close physical and emotional dependence on the mother must wane and the young animal must acquire the dispositions, knowledge, and specific social skills that it requires to perform as an adult member of the community" (Mason 1973:20).

The question that arises regarding the Belize howlers is concerned with when and how the mother-infant bond loosened to allow the infant to pass from one task to the other. Mason (1973) suggests that the trend which takes the infant away from the mother and brings it into contact with the larger world is already present in early infancy, although it is overshadowed by the infant's responses to seek contact with the mother. This trend, of course, has been shown to differ greatly between species. In bonnet macaques (Macaca radiata), for example, infants associate with group members other than the mother from a very early age, whereas infants of pigtail macaques (Macaca nemestrina) remain close to their mothers for a much longer period of time (Rosenblum and Kaufman, 1967).

The study on the howler groups in Belize revealed a steady trend away from the mother with age of an infant (figures 1, 2). The transition started with short excursions which became progressively longer as the infant became less dependent on nursing and thermoregulation and acquired better coordination of its movements. The results clearly indicate that the progressive decrease in mother-infant interactions is counterbalanced by a steady increase in the infant's interactions with its physical environment (figures 1, 2). The data from the three age classes show that older infants interacted more frequently and for longer periods of time with the physical environment than younger

ones.

The extent to which this process of getting acquainted with the outside world is due to the mother's role or that of the infant is disputed, and has been shown to be dependent on the particular species under investigation. Hinde and Spencer-Booth (1967) suggest that the mother and infant have an equal role in the development of independence of an infant. Jensen, Bobbit, and Gordon (1967) found that pigtail macaque mothers play an active role in instigating independence by leaving their infants for periods of time, increasing punishment and decreasing cradling behaviors, or employing species-specific facial expressions. These authors suggested that the infants responded to the instigation of independence by utilizing the physical environment in a process that begins early and is continuous.

In the Belize groups the process of independence was continuous (figures 1, 2). Observations suggest, however, that it was predominantly the infant's curiosity which brought about more and more interactions with the physical environment as the infant became stronger and more coordinated. Apart from the mother's tendency to be very permissive toward her infant and her habit of bringing her infant in close association with other group members, subtle cues administered by the mother may to some extent have directed the infant to interact elsewhere.

Interactions with 'others'

Once the trend away from the mother is initiated, infants of different species may interact to various degrees with other group members and with the physical environment. In small groups, primarily those exhibiting monogamous grouping patterns, interactions with other group members are limited and interactions with the physical environment

are likely to take their place. However, I also consider an infant's personality and the way it relates to members of its group instrumental in the resulting patterns of interactions.

The results on the Belize groups have shown (figures 1, 2) that infants interacted with group members other than the mother from a very early age (age class I), and this pattern remained fairly constant throughout infancy regarding both frequency and duration of interactions. The only exception was an increase in the duration of interactions between infants of age class III and group members other than the mother. This trend of an infant's early association with other group members reflects the great permissiveness of howler mothers, who, in fact, promoted interactions as seen in cases where howler mothers deposited their young infants close to other group members, then retreated to feed or to howl. The 'tolerant' and non-aggressive attitude of all group members toward infants does not give a mother reason to be restrictive as is the case in some other species, for example, rhesus monkeys (Macaca mulatta). Hinde et al. (1964) have observed that the presence of a possessive 'aunt' in a rhesus group, who continually tried to steal infants from their mothers, greatly increased the restrictiveness of mothers toward their infants. My own study on the white-fronted capuchin (Cebus nigrivittatus) showed that the constant attempts of an adult female to touch, groom, and abduct the infant caused the mother to become very restrictive and aggressive. The mother also frequently directed aggression to the adult male who showed great interest in the infant.

Although there was no change among age classes in the frequency with which infants of the Belize groups interacted with group members other than the mother, an infant of age class III spent more time with

'others'. An infant of this age no longer nursed, and locomoted independently. For this reason frequent contact with the mother was no longer as important as it was at a younger age. These conditions permitted an infant to interact for longer periods of time with group members other than the mother.

Interactions with the adult male

Among primates, a great range of behavior between adult males and infants is found. This range relates not only to the intensity of the male-infant bond but also to the onset of contact between males and infants. Thus, for example in marmosets, an adult male has been seen to exhibit parental behavior immediately following the birth of the infants, and, in fact, has been observed to assist during the birth of infants (Redican, 1976). The carrying of infants in this species continues even after the infants have been weaned (Langford, 1963; Mallison, 1971). Epplé (1975) observed that in the brown-headed tamarins (Saguinus fuscicollis) the adult males carry the infants more during the first months of their lives than later. Wendt (1964) reported that in a group of cotton-top tamarins (Saguinus oedipus) the male carried the offspring exclusively during the first 5 weeks of life; later the mother participated in the carrying. The next offspring, however, remained with the same female for one week after its birth before the male and siblings participated in its care. In other monogamous species, such as gibbons (Hylobates) and siamangs (Symphalangus), on the other hand, although interactions occur among males and the very young offspring (Carpenter, 1940), they become more prominent as the infant becomes less dependent on its mother (Berkson, 1966; Chivers, 1971, 1972).

Studies on different species of Alouatta have shown that in

Alouatta palliata (Baldwin, 1980, pers. comm.), Alouatta seniculus (Neville, 1972a), and Alouatta caraya (Shoemaker, 1979), the male-infant bond is very loose, and characterized by few interactions which are generally initiated by the infants with little active participation by the adult male. In all three species, however, a trend has been observed toward an increased number of interactions with the male as the infant matured. Neville (1972) and Carpenter (1965) remarked on the higher frequency of interactions between older infants and adult males, especially regarding play activities and some sexual behavior.

The results of the Belize study indicated that with age of the infants there was a strong trend toward more and longer lasting interactions with males (tables 31, 32). The infants' greater mobility at a more advanced age was certainly instrumental in the increase of contacts, although the tendency of adult males and females to congregate in close physical association already brought very young infants into the close vicinity of adult males.

The above has shown that the onset of male parental behavior differs among species and even within the same group as subsequent infants are born. With respect to change in patterns of male parental behavior in the course of infancy, the situation as it exists in the Belize groups is reminiscent of that in gibbons and siamangs where male-infant interactions already occur between males and very young infants but increase as the infant matures. In monogamous New World species other than Alouatta the male-infant bond is generally strong soon after an infant's birth and may decline with age of an infant.

Peripheralization

In order to maintain a monogamous group, it is necessary for

animals approaching adulthood to leave the group. Studies on monogamous species (Epple, 1967; Fitzgerald, 1935; Hampton et al., 1966) have shown that this event is achieved by a process known as peripheralization. In this process animals approaching maturity are forced to leave the group or stay at its periphery.

Peripheralization has not been well studied in any primate species to date. This process has been reported as aggressive in marmosets (Epple, 1967 and others). In gibbons the process of peripheralization has also been described as aggressive by Carpenter (1940) and Ellefson (1968). As young gibbons approach maturity, they are threatened by both parents and eventually leave the troop. In siamangs, peripheralization is more gradual (Chivers, 1971, 1972; Fox, 1972, 1974), and may occur primarily during the gestation or birth of subsequent offspring when tension among adults is highest (Fedigan, 1980).

It is not known what form peripheralization takes in monogamous howler groups. In the present study, attempts were made to define whether there were incipient indicators pointing to the gradual initiation of this process toward the end of a young howler's infancy. The results (table 33) show that adult and juvenile group members are not significantly more inclined to terminate an interaction initiated by an infant of age class III than that of a younger infant. Possibly, however, in the non-aggressive howlers the adult does not terminate an interaction in a manner visible to an observer. Perhaps an adult communicates his unwillingness to interact using subtle cues. The higher frequency and longer duration of an older infant's interactions with the physical environment may be testimony to the process of peripheralization. Only in groups II and VI were mothers sometimes

openly refusing to interact with their respective infants - FI_3 in group II, MI_2 in group VI - by moving a short distance away. Males were seen more often to terminate an infant's interaction.

The presence of late juvenile males and females in some of the Belize groups indicates that the process of peripheralization may occur very late or in some cases - as in group I and VI where group members were permitted to remain in the group after they had reached sexual maturity - may not be enforced. In groups II (FJ_2) and V (FJ_2) in Belize and in group II (MJ_2) in Tikal, however, the late juvenile sometimes left the group for extended periods of time to rejoin it later. Overt types of peripheralization of late juveniles was never observed in Belize, while in Tikal the following incident may have been an attempt to peripheralize the MJ_2 in a more aggressive manner:

Jan. 13, 5:15 PM: Howler group II, consisting of 1 AM, 1 AF, 1 MJ_2 , and 1 FJ_1 (see table 1) had been foraging for about an hour. The two juveniles had disappeared for extended periods of time foraging on their own. Shortly after 5:00 PM, the AM, AF, and FJ_1 settled down for the night in a large ramon tree. After 10 to 15 minutes the MJ_2 appeared in the vegetation, heading toward the ramon tree. As he reached the outer branches, the AM got up and moved toward the MJ_2 . The animals faced one another at a distance of approximately one meter (15 meters up in the tree). The MJ_2 started to grunt in a low voice. After about 10 minutes the grunting was replaced by very loud howling. The AM joined in the howling concert. The two animals faced one another for 35 minutes, the AM standing stiff-legged, the MJ_2 slightly crouching. Finally the AM stopped howling; a few seconds later the MJ_2 stopped as well. The AM retreated to his resting spot higher up in the tree. The MJ_2 followed and settled down for the night in the upper canopy.

The group was not encountered thereafter, and it could not be determined when or if the MJ_2 left the group.

Summary - The Age Class

Changes were seen to occur in the course of a young howler's infancy. The gradual loosening of the mother-infant bond is related inversely to the infant's increasingly more frequent and longer-lasting interactions with the physical environment. Little change was detected in the frequency of interactions between an infant and group members other than the mother, although they lasted somewhat longer for an infant of age class III (table 30). Adult male - infant interactions increased progressively with the age of the infant. Although direct evidence of peripheralization was not obtained during late infancy, a greater reluctance of group members to engage in interactions with older infants, combined with the infant's increasingly stronger orientation toward its physical environment, may have been early indicators of peripheralization.

Changes that occurred in the course of a young howler's infancy reflect parental caretaking patterns in this species. The gradual loosening of the mother-infant bond, and orientation of infants toward the physical environment, which in the Belize groups was in no instance accompanied by agonistic behavior, points to a very relaxed and permissive relationship between mother and infant. The same permissive attitude was evident in the interactions between infant and 'others'; infants interacted freely with group members other than the mother from a very early age. The male's participation with, and interest in, the young infant reflects this tendency of tolerance and accommodation that became more prominent as interactions within this dyad increased with an infant's age.

Whether peripheralization was incipient or not at the end of

infancy, the howler infant performed the two important tasks postulated by Mason (1973) - maintaining contact with the mother and preparing itself to function as an adult - in a smooth, coordinated manner, in co-operation with the other members of its group.

CHAPTER SIX

THE SPECIES

RESULTS

In this section, generalizations are abstracted at the level of the species. The behavior of all infants is lumped (tables 34, 35) and the resulting proportions are considered representative of the 'average' pattern of parental behavior. This procedure facilitates comparisons of the results from this study with results of other species for which age categories are not specified and for species that have different maturation rates. A presentation at this level of abstraction does not account for individual or even class differences. For this reason, individual cases are cited, in addition to the species norm, where this procedure is warranted by the particular comparison.

1. Average Behavioral Profile

Tables 34 (frequency) and 35 (duration) represent the average behavioral profiles of a howler infant. Regarding the frequency of interactions, the infant spent 37 % with its mother, 32.1 % with other group members (11.4 % with males, 7.7 % with females, and 13 % with infants), and 31.0 % with the physical environment.

The time variable expressed in the behavioral profile (table 35) indicates that a howler infant spent 58.1 % of the day (daylight hours) interacting with its mother, 16.9 % with group members other than the mother (5.5 % with males, 3.7 % with females, and 7.7 % with infants), and 25 % with the physical environment. The discrepancy in the frequency and duration of interactions stems from the fact that an infant tended to interact for different lengths of time with the

respective group members. An interaction with the mother lasted on the average 14.3 minutes, with a male 4.4 minutes, with a female 4.4 minutes, with an infant 5.4 minutes, and with the physical environment 7.4 minutes.

2. Patterns of Social Interactions

Lumping of all the frequencies (table 36) and the duration (table 37) within each category of behavior - clinging, affiliation, and play - shows to what extent and in which way a howler infant interacted on the average with members of its group.

Clinging

Clinging was largely restricted to the mother-infant dyad (91 % for frequency, 98.6 % for duration). Occasional interactions of this type were seen between males and infants or between infants and other group members (tables 36, 37; figures 3, 4).

Affiliation

In these behaviors, the mother-infant dyad again showed the strongest ties (53.3 % for frequency, 56.4 % for duration). Male-infant interactions of this type of behavior, however, were high, amounting to 27.2 % for frequency (which constitutes roughly half of the affiliative interactions between mother and infant), and 25.9 % for duration. The proportion of interactions between infant and females was lower (14.1 % both for frequency and duration; tables 36, 37), and even less affiliative behavior was seen among infants (5.5 % for frequency, 3.6 % for duration; figures 3, 4).

Play

Although a fair proportion of play interactions occurred among infant and mother (26.1 % for frequency; 22.5 % for duration), infant

and males (16.8 % for frequency, 10.1 % for duration), and infant and females (14.8 % for frequency, 10.4 % for duration), they were most prevalent among peers (42.3 % for frequency, 57 % for duration; see tables 36, 37).

The types of interactions which best characterize a dyad are shown in the column percentages of tables 36 and 37. The close mother-infant bond related mainly to clinging (50.4 % for frequency, 80.3 % for duration) and affinitive behavior (30.2 % for frequency, 14.9 % for duration). Male-infant interactions were predominantly of the affinitive type (50.6 % for frequency, 72.0 % for duration), followed by play behavior (41.0 % for frequency, 22.6 % for duration). The female-infant bond was marked by short play bouts (53.3 % for frequency, 34.7 % for duration) and fewer but longer lasting affinitive interactions (38.3 % for frequency, 58.3 % for duration). The relationship between peers was characterized by an overwhelming proportion of play interactions (89.0 % for frequency, 91.4 % for duration).

Tables 36 and 37 further indicate that of a total of 2165 social interactions between infants and other group members, an infant interacted on the average 53.6 % with its mother, 16.4 % with males, 11.1 % with females, and 18.9 % with other infants. Regarding the time spent in social interactions (based on a total duration of 357 hours), a howler infant passed on the average 77.4 % with its mother, 7.4 % with males, 4.9 % with females, and 10.3 % with infants.

3. Initiator - Receiver - Terminator of Interactions

During observations of the six howler groups in Belize, one behavioral characteristic was especially striking. In all groups,

the infant(s) initiated an overwhelming proportion of the interactions. In order to determine to what extent interactions were occurring due to the initiative of infants or adults, the initiator, receiver, and terminator of each interaction was recorded.

Table 38 indicates that out of a total of 3138 interactions involving infants, 2777 (88.5 %) were initiated by infants. The remaining 361 interactions (11.5 %) were initiated by group members other than infants but were directed toward infants. The infants thus were the receivers of 11.5 % of all interactions. Regarding the terminations of interactions (normally an interaction was terminated when one of the animals involved left or stopped doing whatever it was engaged in), the infants were responsible for a total of 2437 (77.6 %).

DISCUSSION

Seyfarth et al. (1978:49) commented on the importance of abstracting generalizations across an increasingly wide number of cases:

Beginning with descriptions of social relationships and their patterning in one group, we should be able, in future, to produce descriptions of social relationships common to a number of groups and from this point proceed to a more important goal, namely, the formulation of organizational principles which can explain regularities across groups and across species.

The objective of this section of the discussion is to compare parental behavior in monogamous groups of Alouatta palliata pigra to observations in polygamous and polygynous groups of Alouatta, as well as to parental behavior in other species of non-human primates, primarily those exhibiting monogamous grouping patterns. The lack of comparable quantitative data in the primate literature allows only general comparisons mainly of qualitative observations.

Interactions with the mother

Studies on parental care in Alouatta (Altmann, 1959; Baldwin and Baldwin, 1973; Carpenter, 1964; Neville, 1972a) refer to the close mother-infant bond and the accommodative behavior of the mother toward her offspring. This tendency of showing tolerance toward an infant is evident in all howler species studied. Neville (1972a) remarked on the very permissive attitude of howler mothers (Alouatta seniculus) in Venezuela. My own study on Alouatta seniculus in the Frankfurt Zoo showed that even a very sick howler mother, suffering from abdominal pains, was always ready to accommodate her rather rambunctious 10 months old female infant. When the infant jumped on the ailing mother, she responded by putting her arm around it, hugging the infant. The mother was rather irritable and openly showed her unwillingness to interact with the adult male and the subadult female, but in no instance did she reject her infant.

My observations on the howlers in Belize agree with the findings of the above authors. A howler infant in Belize spent on the average slightly more than half of the daylight hours with its mother (58 %) and shared with her 37 % of the total amount of interactions (tables 34, 35). The mother was accommodative at all times, and even prolonged and intensive interactions such as jumping on the mother's back - sometimes intensified by the efforts of a peer - never led to aggressive encounters and seldom caused the mother to get up and leave. Different investigators (Carpenter, 1965 and others) have observed that a howler mother's permissiveness not only relates to associations between her and her infant but also becomes prevalent in interactions between her infant and other group members. Carpenter (1965) observed that a mother allowed

other females to touch her young one immediately after birth. Neville (1972a) recorded a transfer from mother to another female for an infant less than 11 days old; the infant remained with the other female for at least 24 minutes. Altmann's (1959) observations agree with those of the above investigators excepting one occasion when he saw a mother quickly carrying away her infant at the approach of other animals of the group.

In the Belize groups the mothers not only allowed their infants to interact freely with all group members on their own initiative, but frequently promoted interactions between their infants and others. Mothers sometimes sat down close to other animals of the group, a positioning which resulted in an infant's immediate transfer from the mother's back to that of the adjacent animal. In group III the mother trusted her small uncoordinated infant to the care of an older infant when she went off to howl and feed. In rough-and-tumble play between peers, it was surprising to see that a mother would not interfere when her small infant₁, which was still rather uncoordinated in its movements, engaged in acrobatics with an older infant. The older infant often vigorously pulled the smaller infant from the branchlets it was clinging to, and the young infant's lack of coordination was evident as it jerkily tried to grasp another branchlet with its tiny hands, sometimes falling several feet before grasping a branch. My observations revealed that a mother left it up to her infant to decide how far it dared to venture. The infant seemed to develop a good judgement from a very young age, and although often adventurous, showed caution where it could not cope with the situation. Several times it was observed that a small infant did not dare to walk across a large slippery branch of

a fig tree in order to catch up with its mother. The mother was seen waiting for the infant, then walked back a few steps trying to encourage the infant to come to her. Frequently the mother had to return to the infant, to take it across on her back.

Regarding the relationship between a mother's permissiveness and an infant monkeys's drive for activity, an interesting argument was given by Brazelton (in Hinde and Simpson 1975:60). He states: "The mother does everything for an infant who is more passive and who lies at the mother's feet after birth waiting for her to take care of him. The more active babies engender a passive response in their mothers and it looks as if the mothers are responding to that behavior". To what extent the permissive attitude of mothers is due to the great activity of the howler infant is not quite clear. My observations lead me to suggest, however, that the permissive behavior of the mother reinforces the infant to engage in activities, while in turn, the behavior of the very active infant exerts influence on the mother. Thus, in howlers, this behavior seems to be based on reciprocity.

Descriptions of the great permissiveness of howler mothers are often accompanied by descriptions of little overtly affiliative behavior on the part of the mother (Baldwin and Baldwin, 1973; Carpenter, 1964; Neville, 1972). In my study groups, affiliative behavior between mother and infant was considerable compared to reports from the literature (tables 36, 37; figures 3,4). Affiliative interactions were usually initiated by the infant. The infant approached the mother, whereupon the mother put her arm around the infant, hugging and muzzling it. While interacting in an affiliative manner, the mother at times seemed to be aloof, while at other times she was fully engaged, playing

with, hugging, or muzzling the infant.

Thus, apart from the more active participation of the Belize howler mothers in interactions with their infants, parental behavior as administered by the mothers in Alouatta palliata pigra closely resembles that of other howler species.

Interactions with the male

Reports from the literature have shown that active participation in the upbringing of the young and even predominance in this activity on the part of the father is common in monogamous groups (Redican 1976, and others). Although variability regarding the degree to which the father participates does exist among species (Crandall, 1951; Epple, 1975; Hill, 1957; Redican, 1976; Sanderson, 1957) and even among different groups of the same species (Epple, 1975), parental behavior as exhibited by the adult male is integral to the raising of offspring in monogamous groups. The question initially raised in this study centered on the issue of participation of the male howler monkey in the raising of the offspring in monogamous groups of Alouatta palliata pigra.

Observations of male care in the Belize howlers have shown that although the proportions in the frequency of male-infant interactions are high in certain types of behaviors (27.2 % for the frequency, 25.9 % for the duration of affiliative interactions, see tables 36, 37; figures 3, 4), the overall percentage of male-infant associations is lower (16.4 % for frequency, 7.4 % for duration). A loose comparison between these values and the situation as it exists in monogamous groups where the male often takes the predominant role in the upbringing of the young, shows a considerable difference (e.g., Epple 1975). The

reason for this difference in contact is mainly due to the fact that male howlers in Belize were never observed to carry infants, an activity which accounts for a high percentage of male-infant associations in monogamous New World species. Recent studies (Kleiman, 1977; Leutenegger, 1973) have shown that the birth weight of the newborn infant in relationship to the mother's weight is a decisive factor in male care in many monogamous species. Mitchell (1979) asserts that, the larger the infant at birth, and the smaller the mother, the more immediate is the male attention to infant care. The mother-infant weight relationship in howlers is such that the mother does not depend on the male for carrying the infant. Not only is the howler infant considerably smaller at birth in relation to the mother's size than is the case in other monogamous New World species, but howlers only give birth to one infant at a time, while in other monogamous New World species twins are the rule.

Male parental behavior in Alouatta palliata pigra resembles that in other species of howler monkeys in certain aspects. A high degree of tolerance toward infants, combined with little active participation on the part of the male, has been remarked upon by Baldwin and Baldwin (1973), Carpenter (1964), Didur (1980), and Neville (1972a). Males are, however, known to interfere actively in case of danger. Carpenter (1964:88) states that "in general, males behave indifferently to young animals, but they may assist in retrieving infants, protect them from predatory animals, and in unusual situations care for an infant in somewhat the same way as a mother". In one regard, Carpenter's observation does not parallel the situation as it was found in Belize, where males participated more actively in infant care. A male's

accommodative behavior toward infants and his cooperative attitude in unusual situations, however, finds close agreement in the Belize groups. In the black howlers of Belize, the alertness of adult males and their cooperation in parental care became obvious when males took care of infants while females were foraging, and also in situations of stress, as in the case of the small MI_1 in group I which was abandoned by the female caretaker in the upper canopy. The adult male in group III in Tikal also showed great concern and cooperation in parental care when a subadult female spider monkey harassed the female infant₃.

Carpenter (1964) made the interesting observation that despite the rare close physical contact between males and infants, young howlers orient themselves in reference to the adult males. This type of behavior was not recorded in Belize, since it was in many cases difficult to assess from a distance because visual cues figure prominently in this type of behavior. In groups III and IV I observed, however, that the male infants of age class III oriented themselves in reference to the adult males, as they followed the males during group progressions, and foraged and sat in their close vicinity.

The great variety of male caretaking patterns which is evident even between different groups of the same species - as in the Belize groups - has led to questions concerning the factors which are instrumental in the formation of male parental care. Genetic predisposition for parental care in Alouatta is suggested by Carpenter in his statement (1964:88) that "in unusual situations males care for an infant in somewhat the same way as a mother". A potential for infant care in males was obvious in the Belize groups where males cared for infants while mothers were foraging.

Mutual attraction between male and infant is another factor that deserves consideration. Mitchell's (1979:185) observation: "Some howler males become attached to specific infants and allow them to hold onto their ventral surfaces and may carry them in this position for short distances", supports this suggestion. In the Belize groups, males were seen to hold, hug, and muzzle infants which ran into their arms while the mother was nearby. In this case there was no need for a caretaker, and it seemed that attraction between the animals led to the affiliative encounters.

The observation that learning is important in parental care has been made by Epple (1975). In group III in Belize, for example, the MI_3 was exposed from a young age to the care of an infant. Apart from its mother and the adult male, this MI_3 was the only group member that was available for interactions with the MI_1 as well as for alloparenting when the mother went off to howl with the adult male. In turn, this MI_3 spent more time with the adult male than any other infant (table 6). Possibly male care in this small group, where only one female was present, has perpetuated itself through learning. The question arises whether in the presence of a female caretaker, the MI_3 would associate to the same degree with the small MI_1 . The situation as encountered in group IV showed that even in the presence of three females (two FJ_2 , one FJ_1) as compared to two males (one AM, one MJ_2), the MI_3 interacted more with the males both in frequency (28.3 %) and duration (19.7 %) than with the females (9.8 % for frequency, 12.6 % for duration) (tables 9, 10). Thus, the presence of females may not determine or even influence male-infant interactions. The above indicates that various factors may contribute to the intensity of male care that is found in

a group.

Interactions with females other than the mother

Relationships between infants and females (AF , FJ_2 , FJ_1) have been shown to differ in the various studies where such are described. Neville (1972:57) reports that the above categories of females "often but not always showed interest in the recent infant of another adult female through overt approaches, attempts to touch and attempts to induce transfers, and infants as old as 10 weeks were still interesting to other females". Carpenter (1965) observed that a newborn infant is very attractive to other females, especially those without infants; they cluster around the infant, exploring, touching, and muzzling it. As the infant grows, it becomes less attractive for other females, particularly in groups where there are many infants. Where there are few infants, females without infants may be closely and fairly constantly associated with the infant-mother dyad. The Baldwins (1973), on the other hand, observed in an area of very high population density in Panama that the small infants did not attract much attention in the troop. "Occasionally an adult female would come up to a mother and gaze at her infant and sometimes touch the mother, but none were ever observed to touch or hold an infant" (Baldwin, 1973:41). My observations on a small group of Alouatta seniculus in the Frankfurt Zoo revealed that interactions between the FI_3 and the subadult female were the most frequent dyadic interactions in the group (43.5 % of the total). This high frequency may be due to the caged condition, and also to the fact that the subadult female acted as playmate, as seen in many vigorous and long-lasting play bouts, and at the same time as caretaker.

The pattern that emerges from the above studies suggests that

more female-infant interactions occur in groups where only few infants are present as compared to groups with many infants. My observations in Belize, however, do not fit into this pattern. In the small howler groups where only one or at most two infants were present, the females did not show overt interest in the infants. They rarely initiated interactions, and overall rated lowest in frequency and duration of interactions (tables 36, 37). All females in the six study groups in Belize, however, were very tolerant of the infants, allowing them to jump on and climb over their backs many times. Adult females in group I frequently took care of one another's infant, and this activity was also observed in group VI. Characteristically the female, after seeing her infant play with its peer in close vicinity of the other female, took off at a high speed to feed in the outermost branches. Whether she did not dare to venture into this low part of the vegetation, where leaves were most plentiful, with her small infant, or whether she enjoyed the freedom for a while, could not be determined.

Interactions with peers

Interactions among infants are only discussed in as far as they reflect parental caretaking strategies.

The average behavioral profile of howler infants (tables 34, 35) as well as the patterns of interactions (tables 36, 37) show that in both the frequency and duration of contact, peer interactions rate next to mother-infant interactions. Tables 36 and 37 (figures 3 and 4) further indicate that an overwhelming proportion of peer interactions consist of play behavior.

Howler infants engage in play activities frequently and for long periods of time. Carpenter (1965:282) remarked that "an infant spent

on the average 80 % of its waking time playing". In Belize play activities with both animals active started when the infant was between 2 and 4 months of age. At the age of 2 months (MI_1 in group III) play activities were primarily restricted to the manipulation of parts of another animal's body. At 4 months (MI_1 in groups I and VI), the small infants were already participating in rough-and-tumble play, although their movements were still rather uncoordinated, and falls into a lower part of the vegetation were seen. Despite the fact that the small infants were engaging in rough-and-tumble play where they seemed to be barely withstanding the more vigorous approaches of the older infants, at no time was an adult or older juvenile seen interfering in the play activities. Parental attitudes toward peer play very much reflect the permissiveness so prominent in the Belize howlers.

Interactions with the physical environment

The results have shown that a howler infant engaged frequently and for a considerable length of time in interactions with its physical environment (tables 34, 35). Neither the mother nor any other group member was ever seen restraining an infant or bringing it back from its explorations. This observation coincides with the situation encountered by the Baldwins (1973) in Panama, where howler mothers rarely restrained their infants. Altmann (1959) and Carpenter (1934), on the other hand, indicated that mothers were seen to restrict their infants from locomoting away from them and from exploring the vegetation. In the Belize groups, even infants of age class I (with the exception of the MI_1 in group III) ventured to distances of up to 8 meters from their mothers, returning at their own initiative.

Infant's Role in Making and Breaking of Contact

The preceding discussion has shown that adult and subadult group members leave it largely to the initiative of infants to engage in social and non-social interactions. The results have indicated that the infants in the Belize groups were responsible for an overwhelming proportion of initiations and terminations of interactions.

Hinde (1975), in his study on mothers' and infants' roles in the making and breaking of contact, suggested that the difference between the percentage of 'makes' due to the infant and the percentage of 'breaks' due to the infant, provides a measure of the infant's role in contact. Hinde further explained that if the infant is responsible for a higher percentage of 'makes' than of 'breaks', he has the greater role; while if he is responsible for more 'breaks' than 'makes', the mother would have the major role. The results of the Belize study show, that, according to Hinde's scheme, the howler infant has the greater role in the established contact between itself and other group members.

There are some difficulties involved in determining which animal is the initiator or terminator of an interaction. Observing from a distance, the only way to judge is to define that animal as initiator which walks toward another or makes the first visible move. The animal which is believed to be the initiator could, however, respond to signals from its partner which are not recognizable to the observer, such as subtle visual, vocal, or tactile cues. Despite a possible factor of error, however, the general impression one gets while observing patterns of interactions in the Belize howlers is that of a very active infant and of a much more passive adult.

Summary - The Species

Parental behavior exhibited in the monogamous howler groups in Belize differs from that in other monogamous species, and also from polygamous and polygynous species of howlers in some respects.

The mother-infant bond is close in all howler species studied. The mother is accommodative and permissive toward her infant, and her permissive attitude is believed instrumental in promoting early independence in the infant, while the infant's high degree of activity and alertness, in turn, may engender a more passive response in the mother. Howler mothers in the Belize groups, however, participated more actively in interactions with their infants than has been reported from the literature. The mother-infant bond in monogamous groups of Alouatta is a closer one than that in other monogamous species in which the male engages to a greater degree in infant care, mainly carrying activities.

Male-infant interactions are more pronounced in the monogamous groups of Alouatta palliata pigra in Belize than in polygynous and polygamous groups of Alouatta elsewhere. They are, however, on the average less expressed than in other monogamous New World species because male howlers do not normally carry infants, although in two groups (III and IV), male participation in other interactions exceeded that of the mother in either frequency or duration (tables 9, 10). Male care in the Belize groups most closely resembles male care in gibbons and siamangs, where the male starts interacting with the very young infant and becomes more involved as the infant matures. Male parental care in howlers, I believe, arises due to a certain predisposition toward this behavior combined with attraction between male and infant and/or exposure to learning infant care. Male parental care is also characterized

by a highly permissive element.

Interactions between infants and females other than the mother are fewer than among other age-sex classes, and marked by the same permissive attitude that characterizes mothers and males.

Peer interactions, which are sometimes promoted by mothers and other females with infants, are biased toward play activities. Very young infants engage in rough-and-tumble play without interference by an adult. The permissive attitude of the adult howlers manifests itself also in an infant's interactions with the physical environment. Adults were never seen to restrain an infant from wandering off. The adult howlers' great potential for permissiveness, and to some extent passiveness, is complemented by the infants' high level of activity. Infants are the predominant initiators of interactions and are thus primarily responsible for establishing contact.

CHAPTER SEVEN

CONCLUSIONS

This section focuses on three major issues pertinent to parental behavior in Alouatta palliata pigra that were postulated at the beginning of the study and/or arose during the course of observations.

1. How does parental behavior in monogamous groups of Alouatta palliata pigra compare to parental behavior in other species of the genus Alouatta and to monogamous species elsewhere?
2. How does parental behavior, as it was encountered in the monogamous groups of howlers in Belize, affect group life?
3. What is the adaptive value of this type of parental behavior within the habitat of Alouatta palliata pigra in Belize?

1. Parental Behavior in Alouatta palliata pigra - its relationship to other species of howlers and to monogamous species elsewhere.

The question initially posed relates to the extent to which parental behavior in monogamous groups of Alouatta palliata pigra would resemble the situation in other species of the genus Alouatta and/or monogamous species elsewhere. Although this question is far from resolved, this study has shed light on certain aspects.

Parental behavior in the monogamous groups of Alouatta palliata pigra, although similar to parental care in other species of howlers (see discussion on species), differs in some aspects. Male parental behavior is more expressed in Alouatta palliata pigra than in other species of Alouatta, but it is less developed than in monogamous species elsewhere, with the possible exception of gibbons and siamangs. Male

care and other aspects of parental behavior show a high degree of individual variability.

Inter-individual variability - so pronounced in the Belize howler groups - may be the decisive element that underlies the potential for plasticity for which howler groups are generally known. The fact that Alouatta is found in three different types of groups - monogamous, polygynous, and polygamous - testifies to the potential for change. Most striking of all is the tendency of Alouatta to shift from a polygamous to a polygynous group and back to the former grouping pattern in response to external stress, such as occurred during and after the yellow fever epidemic in Panama in 1951 (Collias and Southwick, 1952). It is not surprising that this potential for plasticity so characteristic in Alouatta should express itself in a great variety of parental behavior patterns.

2. Impact of Parental Behavior on the Group Life of Alouatta palliata pigra.

The most striking aspect of parental behavior observed during the study on Alouatta palliata pigra is the great permissiveness that is extended to an infant by its mother and other group members. A howler infant grows up in a milieu where tolerance is exhibited by all group members and where agonism is minimal. Within an environment of this type, an infant has the opportunity to learn from its group members that in disagreeable situations - for example, an infant jumping relentlessly on an adult's back - it is better to leave than to respond with aggression. The infant thus adopts the same permissive attitude that is demonstrated by group members and thereby gives rise to another

generation of peaceful howlers.

Schneirla (1951) emphasizes the impact of the early social environment on the developing infant, suggesting that differences in early family life may be responsible for the marked contrast between the degree of intragroup aggressiveness in howlers compared with rhesus monkeys. The lack of aggressiveness within howler groups does coincide with the permissive parental behavior. Parental behavior thus not only influences the infant but may affect the character of the social group which, according to Poirier (1972), is related to the strength of inter-animal affinities and to the degree to which relationships are tolerated by other group members. Throughout this study it became evident that tolerance and permissiveness, so prominent in parental behavior in Alouatta palliata pigra, is a predominant feature of the social group.

3. Adaptive Value of Parental Behavior in Alouatta palliata pigra.

The great permissiveness that was extended to howler infants in Belize seemed almost neglectful at first glance. A howler mother allowed her tiny, still uncoordinated infant to wander off exploring the environment, and to engage in vigorous play with older infants. Or, a mother went off to forage, apparently oblivious to her infant, which scrambled to follow her, finally managing to cling to one of her legs, hanging there awkwardly until the mother took a rest. Even at a very dangerous crossing it was left to the infant's initiative to find a ride on one of the group members.

The extent to which this type of behavior is adaptive cannot be fully assessed at this stage. Certain adaptive possibilities, however, do exist. Permissiveness as exhibited by the howlers in Belize may

adjust an infant from a very young age to be alert and to be independent. Apart from encouraging early independence in infants, the permissive parental behavior may be advantageous in reducing aggression within the group. A howler mother permits her infant to interact freely with all group members. This behavior stands in contrast to many species in which restrictiveness on the part of the mother prevails. Thus, for example, in Nilgiri langurs (Presbytis johnii), a mother only permits adult females to approach her infant (Poirier, 1968), while in the ring-tailed lemur (Lemur catta) only the mothers are allowed near the infant (Jolly, 1966). In sifakas (Propithecus) (Jolly, 1966) and vervets (Cercopithecus aethiops) (Lancaster, 1971), mothers have been reported to show aggression toward any animal approaching a small infant. Experiments have shown that after removal of a very possessive pigtail mother (Macaca nemestrina), the infant was unable to adjust to any other group member. An infant that is allowed to interact freely with other group members, on the other hand, has a better chance of survival without the mother. A permissive attitude within a group, often coupled with a loosely structured hierarchy as it exists in howler groups, minimizes or eliminates the risk of injury to the infant by group members. In Alouatta none of the group members are prone to kidnap an infant, as has been reported from wild Campbell's monkeys (Cercopithecus campbelli lowei) (Bourlière et al., 1970) and squirrel monkeys (Saimiri sciureus) (Rosenblum, 1971). Gartlan (1969) reports how vervet infants are sometimes squeezed or pulled apart in disputes between aunts and mothers. In baboon and macaque species, where the hierarchy is structured, infants are used as 'passports' by lower-ranking males to inhibit attacks against them from more dominant animals. Being caught in the skirmish is

dangerous for the infants (Blaffer Hrdy, 1976). Compared to manipulations of this type, a howler infant grows up in a peaceful environment where it can choose with whom to interact and how far to venture. Despite a minimum of parental surveillance, none of the infants in the Belize groups were injured. The Baldwins (1973) also reported a low level of accidents among howler infants in Panama.

Permissiveness, although characteristic of the parental behavior of all species of Alouatta, is most pronounced in Alouatta palliata pigra. It was surprising that, in the most hazardous environment - the territory of group VI -, the infants were raised with the greatest degree of permissiveness, a factor which resulted in their early independence. This situation leads me to suggest that early independence may have been promoted by the parents in a precarious environment that required jumping of wide gaps, crossing of roads and rivers, or foraging through wide areas in search of food.

Parental behavior in the howlers of Belize, despite its apparent neglectful appearance in certain instances, appears to be adaptive within this highly disturbed environment. Since the yellow fever epidemics in the 1950's, the howler populations have increased consistently, testifying to the efficiency of their strategies of survival which are intricately linked to parental behavior.

Table 1. Groups of Alouatta palliata pigra in Tikal

Group	AM	AF	MJ ₂	MJ ₁	FJ ₁	FI ₃	MI ₁	Total
I	1	1	1	1			1	5
II	1	1*	1		1			4
III	1	1	1	1		1		5
	3	3	3	2	1	1	1	14

* = pregnant female

A total of 14 howler monkeys were encountered in the 5 km² area of Tikal.

Table 1 a. Table of Abbreviations

AM	=	adult male
AF	=	adult female
MO	=	mother
MJ ₂	=	male juvenile of age class II (late juvenile)
FJ ₂	=	female juvenile of age class II (late juvenile)
MJ ₁	=	male juvenile of age class I (early juvenile)
FJ ₁	=	female juvenile of age class I (early juvenile)
MI ₃	=	male infant of age class III
FI ₃	=	female infant of age class III
MI ₂	=	male infant of age class II
FI ₂	=	female infant of age class II
MI ₁	=	male infant of age class I
FI ₁	=	female infant of age class I

Age classes agree with Carpenter (1965)

Groups of Alouatta palliata pigra encountered in an area of approximately 7sqkm around Bermudian Landing in Belize

Table 2 Groups with Infants

Group	AM	AF	MJ ₂	FJ ₂	FJ ₁	MI ₃	FI ₃	MI ₂	FI ₂	MI ₁	Total
I	2	2							1	1	6
II	1	1		1			1				4
III	1	1				1				1	4
IV	1	1	1	2		1					6
V	1	1		1				1			4
VI	1	2		1	1			1		1	7
Total	7	8	1	5	1	2	1	2	1	3	31

Table 2a Groups without Infants

Group	AM	AF	MJ ₂	FJ ₂	FJ ₁	MI ₃	FI ₃	MI ₂	FI ₂	MI ₁	Total
A	1	1									2
B	1	1		2							4
C	1	1	2	2							6
D	1	1		1							3
E	1	1			1						3
F	1	1	2								4
G	1	1									2
Solitary male	2										2
Total	9	7	4	5	1						26

Total tables 16 15 5 10 2 2 1 2 1 3 57
2+2a

The sex ratio among the Belize groups is 1:1.

The average group size is 4.4 animals.

The population density is 8.14 howlers per km².

Table 3. The classification of young howler monkeys,
Alouatta palliata

Classifi- cation	Color	Relation to mother	Estimated age ¹		
			Carpenter 1934	Carpenter 1965	Neville 1972
Infant ₁	gray-beige or greyish brown	carried on dorsal and ventral sur- faces of mother	less than 1 month	0-5 or 6 months	
Infant ₂	brownish- black	carried on dorsal sur- faces	about 6 months	5-6 to 10-12 months	
Infant ₃	black	not carried regularly, except at wide gaps and during cool rest periods	about 12 months	10-12 to 18-20 months	ends at about 10- 12 months
Early juvenile	black	separation period: travels near mother but independ- ently	about 18-20 months	begins at 18-20 months	begins at about 10- 12 months
Late juvenile	black, with some red mantle	entirely inde- pendent	about 30-36 months	ends at 50 months	ends at about 2 or 3 years

¹Precise determinations of the chronological ages of howlers have not been made in any of the howler studies. Carpenter's estimates were based on about 8 months of observations on Alouatta palliata on Barro Colorado Island in the Panama Canal Zone. Neville's estimates were based on 13 months of observations on Alouatta seniculus.

Reproduced from Baldwin and Baldwin (1973)

Table 4. Social Interactions
of Infant Howler Monkeys

<u>Categories</u>	<u>Individual Interactions</u>
CLINGING	clinging ventrally while support animal rests clinging dorsally while support animal rests clinging ventrally while support animal moves clinging dorsally while support animal moves
AFFILIATION	sitting in close body contact grooming hugging huddling muzzling touching
PLAY	following in close body contact - playful gait playing - both animals active playing - with part of other group member's body climbing across back - playful gait

Table 4 a. Interactions with the physical environment
(non-social interactions)

<u>Category</u>	<u>Individual Interactions</u>
INTERACTIONS WITH THE PHYSICAL ENVIRONMENT	locomote through vegetation sit and investigate feeding or nibbling on leaves playing with leaves and branchlets playing in vegetation - acrobatics

Table 5. INDIVIDUAL BEHAVIORAL PROFILES

Infants of Age Class I

Frequency

Group	Focal Animal		Mother	Males (AM,MJ ₂)	Females (AF,FJ _{1,2})	Infants	Interact. Environment	Total
III	MI ₁	#	92	7	—	39	6	144
		%	63.9	4.9	—	27.1	4.2	100
I	MI ₁	#	396	90	65	151	244	946
		%	41.9	9.5	6.9	16.0	25.8	100
VI	MI ₁	#	68	13	28	17	66	192
		%	35.4	6.8	14.6	8.9	34.4	100

= frequency of interactions

% = row percentage

Table 6. INDIVIDUAL BEHAVIORAL PROFILES

Infants of Age Class I

Duration

Group	Focal Animal		Mother	Males (AM,MJ ₂)	Females (AF,FJ _{1,2})	Infants	Interact. Environment	Total
III	MI ₁	*	1443.1	7.0	—	178.3	56.3	1684.7
		%	85.7	0.4	—	10.6	3.3	100
I	MI ₁	*	6193.5	217.0	198.1	867.0	1032.0	8507.6
		%	72.8	2.6	2.3	10.2	12.1	100
VI	MI ₁	*	733.5	21.3	116.6	138.8	381.3	1391.5
		%	52.7	1.5	8.4	10.0	27.4	100

* = duration in minutes

% = row percentage

Table 7. INDIVIDUAL BEHAVIORAL PROFILES

Infants of Age Class II

Frequency

Group	Focal Animal		Mother	Males (AM,MJ ₂)	Females (AF,FJ _{1,2})	Infants	Environ- ment	Total
I	FI ₂	#	346	131	76	158	312	1023
		%	33.8	12.8	7.4	15.4	30.5	100
V	MI ₂	#	87	25	19	-	101	232
		%	37.5	10.8	8.2	-	43.5	100
VI	MI ₂	#	63	21	26	15	78	203
		%	31.0	10.3	12.8	7.4	38.4	100

= frequency of interactions

% = row percentage

Table 8. INDIVIDUAL BEHAVIORAL PROFILES

Infants of Age Class II

Duration

Group	Focal Animal		Mother	Males (AM,MJ ₂)	Females (AF,FJ _{1,2})	Infants	Environ- ment	Total
I	FI ₂	*	5373.0	318.1	226.1	752.7	1910.3	8580.2
		%	62.6	3.7	2.6	8.8	22.3	100
V	MI ₂	*	653.1	61.9	64.9	-	566.0	1345.9
		%	48.6	4.6	4.8	-	42.1	100
VI	MI ₂	*	618.9	25.6	73.2	115.4	534.3	1367.4
		%	45.3	1.9	5.4	8.4	39.1	100

* = duration in minutes

% = row percentage

Table 9.

INDIVIDUAL BEHAVIORAL PROFILES

Infants of Age Class III

Frequency

Group	Focal Animal		Mother	Males (AM,MJ ₂)	Females (AF,FJ _{1,2})	Infants	Environ- ment	Total
II	FI ₃	#	29	4	6	-	58	97
		%	29.9	4.1	6.2	-	59.8	100
III	MI ₃	#	23	8	-	28	36	95
		%	24.2	8.4	-	29.5	37.9	100
IV	MI ₃	#	56	58	20	-	71	205
		%	27.3	28.3	9.8	-	34.6	100

= frequency of interactions

% = row percentage

Table 10.

INDIVIDUAL BEHAVIORAL PROFILES

Infants of Age Class III

Duration

Group	Focal Animal		Mother	Males (AM,MJ ₂)	Females (AF,FJ _{1,2})	Infants	Environ- ment	Total
II	FI ₃	*	364.1	12.4	59.4	-	1123.8	1559.7
		%	23.3	0.8	3.8	-	72.1	100
III	MI ₃	*	374.5	413.9	-	153.2	718.1	1659.7
		%	22.6	24.9	-	9.2	43.3	100
IV	MI ₃	*	881.5	499.7	318.8	-	838.8	2538.8
		%	34.7	19.7	12.6	-	33.0	100

* = duration in minutes

% = row percentage

Table 11. PATTERNS OF SOCIAL INTERACTIONS MI_1 - group IIIFrequency

Type of Interaction		Mo	AM	MI_3	Total
Clinging	Frequency	61	1	3	65
	% of Row	93.8	1.5	4.6	100
	% of Column	66.3	14.3	7.7	47.1
	% of Total	44.2	0.7	2.2	47.1
Affinitive	Frequency	4	3	10	17
	% of Row	23.5	17.6	58.8	100
	% of Column	4.3	42.9	25.6	12.3
	% of Total	2.9	2.2	7.2	12.3
Play	Frequency	27	3	26	56
	% of Row	48.2	5.4	46.4	100
	% of Column	29.3	42.9	66.7	40.6
	% of Total	19.6	2.2	18.8	40.6
Total		92	7	39	138
% of Total		66.7	5.1	28.3	100

Table 12. PATTERNS OF SOCIAL INTERACTIONS MI_1 - group IIIDuration (min.)

Type of Interaction		Mo	AM	MI_3	Total
Clinging	Duration	1252	1	5	1258
	% of Row	99.5	0.1	0.4	100
	% of Column	84.9	14.3	2.8	75.9
	% of Total	75.5	0.1	0.3	75.9
Affinitive	Duration	13	2	76	91
	% of Row	14.3	2.2	83.5	100
	% of Column	0.9	28.6	42.9	5.5
	% of Total	0.8	0.1	4.6	5.5
Play	Duration	209	4	96	309
	% of Row	67.6	1.3	31.1	100
	% of Column	14.2	57.1	54.2	18.6
	% of Total	12.6	0.2	5.8	18.6
Total		1474	7	177	1658
% of Total		88.9	0.4	10.7	100

Table 13. PATTERNS OF SOCIAL INTERACTIONS MI₁ - group IFrequency

Type of Interaction		Mo	AM(2)	AF	FI ₂	Total
Clinging	Frequency	239	14	8	0	261
	% of Row	91.6	5.3	3.1	0	100
	% of Column	60.1	15.6	12.3	0	37.1
	% of Total	33.9	2.0	1.1	0	37.1
Affinitive	Frequency	81	36	12	5	134
	% of Row	60.4	26.9	9.0	3.7	100
	% of Column	20.4	40.0	18.5	3.3	19.0
	% of Total	11.5	5.1	1.7	0.7	19.0
Play	Frequency	78	40	45	146	309
	% of Row	25.2	12.9	14.6	47.2	100
	% of Column	19.6	44.4	69.2	96.7	43.9
	% of Total	11.1	5.7	6.4	20.7	43.9
Total		398	90	65	151	704
% of Total		56.6	12.8	9.2	21.4	100

Table 14. PATTERNS OF SOCIAL INTERACTIONS MI₁ - group IDuration (min.)

Type of Interaction		Mo	AM(2)	AF	FI ₂	Total
Clinging	Duration	5818	43	25	0	5886
	% of Row	98.8	0.7	0.4	0	100
	% of Column	93.9	19.9	12.6	0	78.7
	% of Total	77.8	0.6	0.3	0	78.7
Affinitive	Duration	183	69	31	24	307
	% of Row	59.6	22.5	10.1	7.8	100
	% of Column	3.0	31.9	15.7	2.8	4.0
	% of Total	2.4	0.9	0.4	0.3	4.0
Play	Duration	193	104	142	843	1282
	% of Row	15.1	8.1	11.1	65.8	100
	% of Column	3.1	48.1	71.7	97.2	17.2
	% of Total	2.6	1.4	1.9	11.3	17.2
Total		6194	216	198	867	7475
% of Total		82.9	2.9	2.6	11.6	100

Table 15. PATTERNS OF SOCIAL INTERACTIONS MI_1 - group VIFrequency

Type of Interaction		Mo	AM	AF	FJ ₂	FJ ₁	MI ₂	Total
Clinging	Frequency	34	0	0	0	0	0	34
	% of Row	100	0	0	0	0	0	100
	% of Column	50	0	0	0	0	0	27.2
	% of Total	27.2	0	0	0	0	0	27.2
Affinitive	Frequency	19	7	8	3	4	0	41
	% of Row	46.3	17.1	19.5	7.3	9.8	0	100
	% of Column	27.9	58.3	80.0	30.0	50.0	0	32.8
	% of Total	15.2	5.6	6.4	2.4	3.2	0	32.8
Play	Frequency	15	5	2	7	4	17	50
	% of Row	30	10	4	14	8	34	100
	% of Column	22.1	41.7	20.0	70.0	50.0	100	40
	% of Total	12	4	1.6	5.6	3.2	13.6	40
Total		68	12	10	10	8	17	125
% of Total		54.4	9.6	8.0	8.0	6.4	13.6	100

Table 16. PATTERNS OF SOCIAL INTERACTIONS MI_1 - group VIDuration (min.)

Type of Interaction		Mo	AM	AF	FJ ₂	FJ ₁	MI ₂	Total
Clinging	Duration	610	0	0	0	0	0	610
	% of Row	100	0	0	0	0	0	100
	% of Column	83.2	0	0	0	0	0	60.3
	% of Total	60.3	0	0	0	0	0	60.3
Affinitive	Duration	80	15	72	3	6	0	176
	% of Row	45.5	8.5	40.9	1.7	3.4	0	100
	% of Column	10.9	75.0	96.0	14.3	27.3	0	17.4
	% of Total	7.9	1.5	7.1	0.3	0.6	0	17.4
Play	Duration	44	5	3	18	16	139	225
	% of Row	19.6	2.2	1.3	8.0	7.1	61.8	100
	% of Column	6.0	23.8	4.0	85.7	72.7	100	22.3
	% of Total	4.4	0.5	0.3	1.8	1.6	13.7	22.3
Total		734	20	75	21	22	139	1011
% of Total		72.6	2.0	7.4	2.1	2.2	13.7	100

Table 17. PATTERNS OF SOCIAL INTERACTIONS FI_2 - group IFrequency

Type of Interaction		MO	AM(2)	AF	MI ₁	Total
Clinging	Frequency	190	13	8	0	211
	% of Row	90.0	6.2	3.8	0	100
	% of Column	55.1	9.8	10.5	0	29.7
	% of Total	26.7	1.8	1.1	0	29.7
Affinitive	Frequency	84	61	23	14	182
	% of Row	46.2	33.4	12.6	7.7	100
	% of Column	24.3	46.2	30.3	8.9	25.6
	% of Total	11.8	8.5	3.2	2.0	25.5
Play	Frequency	71	58	45	144	318
	% of Row	22.3	18.2	14.2	45.3	100
	% of Column	20.6	43.9	59.2	91.1	44.7
	% of Total	10.0	8.2	6.3	20.3	44.7
Total		345	132	76	158	711
% of Total		48.5	18.6	10.7	27.2	100

Table 18. PATTERNS OF SOCIAL INTERACTIONS FI_2 - group IDuration (min)

Type of Interaction		MO	AM(2)	AF	MI ₁	Total
Clinging	Duration	4627	30	13	0	4670
	% of Row	99.1	0.6	0.3	0	100
	% of Column	86.1	9.4	5.8	0	70.0
	% of Total	69.4	0.4	0.2	0	70.0
Affinitive	Duration	529	128	108	48	813
	% of Row	65.1	15.7	13.3	5.9	100
	% of Column	9.8	40.3	47.8	6.4	12.2
	% of Total	7.9	1.9	1.6	0.7	12.2
Play	Duration	216	160	105	705	1186
	% of Row	18.2	13.5	8.9	59.4	100
	% of Column	4.0	50.3	46.5	93.6	17.8
	% of Total	3.2	2.4	1.6	10.6	17.8
Total		5372	318	226	753	6669
% of Total		80.6	4.8	3.4	11.3	100

Table 19. PATTERNS OF SOCIAL INTERACTIONS MI_2 - group V

Frequency

Type of Interaction		MO	AM	FJ_2	Total
Clinging	Frequency	30	0	1	31
	% of Row	96.8	0	3.2	100
	% of Column	34.5	0	5.3	23.7
	% of Total	22.9	0	0.8	23.7
Affinitive	Frequency	42	11	14	67
	% of Row	62.7	16.4	20.9	100
	% of Column	48.3	44.0	73.7	51.1
	% of Total	32.1	8.4	10.7	51.1
Play	Frequency	15	14	4	33
	% of Row	45.5	42.4	12.1	100
	% of Column	17.2	56.0	21.1	25.2
	% of Total	11.5	10.7	3.1	25.2
Total		87	25	19	131
% of Total		66.4	19.1	14.5	100

Table 20. PATTERNS OF SOCIAL INTERACTIONS MI_2 - group VDuration (min)

Type of Interaction		MO	AM	FJ_2	Total
Clinging	Duration	450	0	3	453
	% of Row	99.3	0	0.7	100
	% of Column	68.8	0	4.6	58.0
	% of Total	57.6	0	0.4	58.0
Affinitive	Duration	159	34	39	232
	% of Row	68.5	14.7	16.8	100
	% of Column	24.3	54.8	60.0	29.7
	% of Total	20.4	4.4	5.0	29.7
Play	Duration	45	28	23	96
	% of Row	46.9	29.2	24.0	100
	% of Column	6.9	45.2	35.4	12.3
	% of Total	5.8	3.6	2.9	12.3
Total		654	62	65	781
% of Total		83.7	7.9	8.3	100

Table 21. PATTERNS OF SOCIAL INTERACTIONS MI_2 - group VIFrequency

Type of Interaction		MO	AM	AF	FJ ₂	FJ ₁	MI ₁	Total
Clinging	Frequency	23	0	0	0	0	0	23
	% of Row	100	0	0	0	0	0	100
	% of Column	36.5	0	0	0	0	0	18.5
	% of Total	18.5	0	0	0	0	0	18.5
Affinitive	Frequency	30	11	3	3	1	1	49
	% of Row	61.2	22.4	6.1	6.1	2.0	2.0	100
	% of Column	47.6	55.0	25.0	60.0	11.1	6.7	39.5
	% of Total	24.2	8.4	2.4	2.4	0.8	0.8	39.5
Play	Frequency	10	9	9	2	8	14	52
	% of Row	19.2	17.3	17.3	3.8	15.4	26.9	100
	% of Column	15.9	45.0	75.0	40.0	88.9	93.3	41.9
	% of Total	8.1	7.3	7.3	1.6	6.5	11.3	41.9
Total		63	20	12	5	9	15	124
% of Total		50.8	16.1	9.7	4.0	7.3	12.1	100

Table 22. PATTERNS OF SOCIAL INTERACTIONS MI_2 - group VIDuration (min)

Type of Interaction		MO	AM	AF	FJ ₂	FJ ₁	MI ₁	Total
Clinging	Duration	446	1	0	0	0	0	447
	% of Row	99.8	0.2	0	0	0	0	100
	% of Column	70.3	4.0	0	0	0	0	52.7
	% of Total	52.6	0.1	0	0	0	0	52.7
Affinitive	Duration	172	16	9	9	1	1	208
	% of Row	82.7	7.7	4.3	4.3	0.5	0.5	100
	% of Column	27.1	64.0	45.0	81.8	2.4	0.9	24.5
	% of Total	20.3	1.9	1.1	1.1	0.1	0.1	24.5
Play	Duration	16	8	11	2	41	115	193
	% of Row	8.3	4.1	5.7	1.0	21.2	59.6	100
	% of Column	2.5	32.0	55.0	18.2	97.6	99.1	22.8
	% of Total	1.9	0.9	1.3	0.2	4.8	13.6	22.8
Total		634	25	20	11	42	116	848
% of Total		74.8	2.9	2.4	1.3	5.0	13.7	100

Table 23. PATTERNS OF SOCIAL INTERACTIONS FI_3 - group IIFrequency

Type of Interaction		Mo	AM	FJ_2	Total
Clinging	Frequency	2	0	0	2
	% of Row	100	0.0	0.0	100
	% of Column	6.9	0.0	0.0	5.1
	% of Total	5.1	0.0	0.0	5.1
Affinitive	Frequency	27	4	5	36
	% of Row	75.0	11.1	13.9	100
	% of Column	93.1	100.0	83.3	92.3
	% of Total	69.2	10.3	12.8	92.3
Play	Frequency	0	0	1	1
	% of Row	0.0	0.0	100.0	100
	% of Column	0.0	0.0	16.7	2.6
	% of Total	0.0	0.0	2.6	2.6
Total		29	4	6	39
% of Total		74.4	10.3	15.4	100

Table 24. PATTERNS OF SOCIAL INTERACTIONS FI_3 - group IIDuration (min.)

Type of Interaction		Mo	AM	FJ_2	Total
Clinging	Duration	15	0	0	15
	% of Row	100	0	0	100
	% of Column	4.1	0	0	3.4
	% of Total	3.4	0	0	3.4
Affinitive	Duration	349	12	54	415
	% of Row	84.1	2.9	13.0	100
	% of Column	95.9	100	91.5	95.4
	% of Total	80.2	2.8	12.4	95.4
Play	Duration	0	0	5	5
	% of Row	0	0	100	100
	% of Column	0	0	8.5	1.1
	% of Total	0	0	1.1	1.1
Total		364	12	59	435
% of Total		83.7	2.8	13.6	100

Table 25. PATTERNS OF SOCIAL INTERACTIONS MI_3 - group III

Frequency

Type of Interaction		MO	AM	MI_1	Total
Clinging	Frequency	2	0	4	6
	% of Row	33.3	0	66.7	100
	% of Column	8.7	0	14.3	10.2
	% of Total	3.4	0	6.8	10.2
Affinitive	Frequency	20	7	6	33
	% of Row	60.6	21.2	18.2	100
	% of Column	87.0	87.5	21.4	55.9
	% of Total	33.9	11.9	10.2	55.9
Play	Frequency	1	1	18	20
	% of Row	5.0	5.0	90.0	100
	% of Column	4.3	12.5	64.3	33.9
	% of Total	1.7	1.7	30.5	33.9
Total		23	8	28	59
% of Total		39.0	13.6	47.5	100

Table 26. PATTERNS OF SOCIAL INTERACTIONS MI_3 - group III

Duration (min.)

Type of Interaction		MO	AM	MI_1	Total
Clinging	Duration	24	0	25	49
	% of Row	49.0	0	51.0	100
	% of Column	8.7	0	16.3	5.8
	% of Total	2.8	0	3	5.8
Affinitive	Duration	242	409	10	661
	% of Row	36.6	61.9	1.5	100
	% of Column	87.7	98.8	6.5	78.4
	% of Total	28.7	48.5	1.2	78.4
Play	Duration	10	5	118	133
	% of Row	7.5	3.8	88.7	100
	% of Column	3.6	1.2	77.1	14.9
	% of Total	1.2	0.6	13.2	15.0
Total		276	414	153	843
% of Total		32.7	49.1	18.1	100

Table 27. PATTERNS OF SOCIAL INTERACTIONS MI_3 - group IVFrequency

Type of Interaction		MO	AM	MJ_2	$FJ_2(2)$	Total
Clinging	Frequency	4	2	2	2	10
	% of Row	40.0	20.0	20.0	20.0	100
	% of Column	7.1	8.3	5.9	10.0	7.5
	% of Total	3.0	1.5	1.5	1.5	7.5
Affinitive	Frequency	44	18	21	17	100
	% of Row	44.0	18.0	21.0	17.0	100
	% of Column	78.6	75.0	61.8	85.0	74.6
	% of Total	32.8	13.4	15.7	12.7	74.6
Play	Frequency	8	4	11	1	24
	% of Row	33.3	16.7	45.8	4.2	100
	% of Column	14.3	16.7	32.4	5.0	17.9
	% of Total	6.0	3.0	8.2	0.7	17.9
Total		56	24	34	20	134
% of Total		41.8	17.9	25.4	14.9	100

Table 28. PATTERNS OF SOCIAL INTERACTIONS MI_3 - group IVDuration (min)

Type of Interaction		MO	AM	MJ_2	$FJ_2(2)$	Total
Clinging	Duration	70	5	4	33	112
	% of Row	62.5	4.5	3.6	29.5	100
	% of Column	7.9	2.1	1.5	10.3	6.6
	% of Total	4.1	0.3	0.2	1.9	6.6
Affinitive	Duration	748	219	230	285	1482
	% of Row	50.5	14.8	15.5	19.2	100
	% of Column	84.8	92.0	87.8	89.3	87.1
	% of Total	44.0	12.9	13.5	16.8	87.1
Play	Duration	64	14	28	1	107
	% of Row	59.8	13.1	26.2	0.9	100
	% of Column	7.2	5.9	10.7	0.3	6.3
	% of Total	3.8	0.8	1.6	0.1	6.3
Total		882	238	262	319	1701
% of Total		51.9	14.0	15.4	18.8	100

Table 29.

Frequencies of Interactions

for the three Age Classes of Howler Monkey Infants

Age Class		Mother	Other Group Members	Environment	Total
I	#	556	410	316	1282
	%	43.4	32.0	24.6	100
II	#	496	471	491	1458
	%	34.0	32.3	33.7	100
III	#	108	124	165	397
	%	27.2	31.2	41.6	100
Total	#	1160	1005	972	3137
% of Total		37.0	32.0	31.0	100

= number of interactions within age class

% = % of row = average percentage of infants of age class

Table 30.

Duration of Interactions

for the three Age Classes of Howler Monkey Infants

Age Class		Mother	Other Group Members	Environment	Total
I	*	8370.1	1744.1	1469.6	11583.8
	%	72.3	15.0	12.7	100
II	*	6645.0	1637.9	3010.6	11293.5
	%	58.8	14.5	26.7	100
III	*	1620.1	1457.4	2680.7	5758.2
	%	28.1	25.4	46.6	100
Total	*	16635.2	4839.4	7160.9	28635.5 min.
% of Total		58.1	16.9	25.0	= 477.3 hrs.

* = duration of interactions in minutes

% = % of row = average percentage of infants of age class

Table 31.

Frequencies of Interactions

for the three Age Classes of Howler Monkey Infants

Age Class		Mother	Males (AM,MJ ₂)	Females (AF,FJ _{1,2})	Infants	Environment	Total
I	#	556	110	93	207	316	1282
	%	43.4	8.6	7.3	16.2	24.7	100
II	#	496	177	121	173	491	1458
	%	34.0	12.1	8.3	11.9	33.7	100
III	#	108	70	26	28	165	397
	%	27.2	17.6	6.5	7.1	41.6	100
Total		1160	357	240	408	972	3137
% of Total		37.0	11.4	7.7	13.0	31.0	100

= number of interactions within age class

% = % of Row = average percentage of infants of age class

Table 32 .

Duration of Interactions

for the three Age Classes of Howler Monkey Infants

Age Class		Mother	Males (AM,MJ ₂)	Females (AF,FJ _{1,2})	Infants	Environment	Total
I	*	8370.1	245.3	314.7	1184.1	1469.6	11583.8
	%	72.3	2.1	2.7	10.2	12.7	100
II	*	6645.0	405.6	364.2	868.1	3010.6	11293.5
	%	58.8	3.6	3.2	7.7	26.7	100
III	*	1620.1	926.0	378.2	153.2	2680.7	5758.2
	%	28.1	16.1	6.6	2.7	46.6	100
Total	*	16635.2	1576.9	1057.1	2205.4	7160.9	28635.5 min.
% of Total		58.1	5.5	3.7	7.7	25.0	=477.3 hrs.

* = duration of interactions in minutes

% = % of Row = average percentage of infants of age class.

Table 33. Percentage of Interactions terminated by the mother,
other females and males. Initiator: Infant.

Initiator		Interactions initiated by the infant		Terminator of Interactions			
Group	Infant			Mother	Females	Males	Total
III	MI ₁	#	123	6	0	0	6
		%		4.9	0	0	4.9
I	MI ₁	#	851	21	5	5	31
		%		2.5	0.6	0.6	3.7
VI	MI ₁	#	172	1	1	3	5
		%		0.6	0.6	1.7	2.9
Age Class I			1145	28	6	8	42 = 3.7 %
I	FI ₂	#	908	9	1	8	18
		%		1.0	0.1	0.9	2.0
V	MI ₂	#	203	9	2	4	15
		%		4.4	1.0	2.0	7.4
VI	MI ₂	#	191	4	4	6	14
		%		2.1	2.1	3.1	7.3
Age Class II			1302	22	7	18	47 = 3.6 %
II	FI ₃	#	87	2	0	1	3
		%		2.3	0	1.1	3.4
III	MI ₃	#	69	0	2	1	3
		%		0	2.9	1.4	4.3
IV	MI ₃	#	174	5	2	4	11
		%		2.9	1.1	2.3	6.3
Age Class III			330	7	4	6	17 = 5.2 %

= number of interactions

% = row percentage

Table 34. Average Behavioral Profile of a Howler Infant
(all age classes lumped)

Frequency of an infant's interactions with:

	Mother	Males (AM,MJ ₂)	Females (AF,FJ ₂ ,FJ ₁)	Infants	Environment	Total
#	1160	357	240	408	972	3137
%	37.0	11.4	7.7	13.0	31.0	100

M, F, and I
lumped = others 32.1 %

= frequency of interactions

Table 35. Average Behavioral Profile of a Howler Infant
(all age classes lumped)

Duration of an infant's interactions with:

	Mother	Males (AM,MJ ₂)	Females (AF,FJ ₂ ,FJ ₁)	Infants	Environment	Total
*	16635.2	1576.9	1057.1	2205.4	7160.9	28635.5 min =
%	58.1	5.5	3.7	7.7	25.0	100 477.3 hrs.

M, F, and I
lumped = others 16.9 %

* = duration in minutes

Table 36. #Average Frequencies of Social Interactions
between a Howler Infant and other Group Members

Behavior	Mother	Males	Females	Infants	Total
Clinging	585	30	19	9	643
% of Row	91.0	4.7	3.0	1.4	100
% of Column	50.4	8.5	7.9	2.2	29.7
% of Total	27.0	1.4	0.9	0.4	29.7
Affinitive	351	179	93	36	659
% of Row	53.3	27.2	14.1	5.5	100
% of Column	30.2	50.6	38.8	8.8	30.5
% of Total	16.2	8.3	4.3	1.7	30.5
Play	225	145	128	365	863
% of Row	26.1	16.8	14.8	42.3	100
% of Column	19.4	41.0	53.3	89.0	39.9
% of Total	10.4	16.7	5.9	16.9	39.9
Total	1161	354	240	410	2165
% of Total	53.6	16.4	11.1	18.9	100

= accumulated frequencies from all 6 groups

Table 37. *Average Duration of Social Interactions
between a Howler Infant and other Group Members

Behavior	Mother	Males	Females	Infants	Total
Clinging	13311	85	74	30	13500
% of Row	98.6	0.6	0.5	0.2	100
% of Column	80.3	5.4	7.0	1.4	62.9
% of Total	62.1	0.4	0.3	0.1	62.9
Affinitive	2475	1134	617	159	4385
% of Row	56.4	25.9	14.1	3.6	100
% of Column	14.9	72.0	58.3	7.2	20.5
% of Total	11.6	5.3	2.9	0.7	20.5
Play	797	356	367	2016	3536
% of Row	22.5	10.1	10.4	57.0	100
% of Column	4.8	22.6	34.7	91.4	16.5
% of Total	3.7	1.7	1.7	9.4	16.5
Total	16583	1575	1058	2205	21421 min = 357 hrs.
% of Total	77.4	7.4	4.9	10.3	100

* = Duration in minutes; accumulated from all 6 groups

Table 38. Proportions at which an Infant on the average initiates, receives and terminates Interactions

Age Class	N u m b e r o f I n t e r a c t i o n s				Total (initiated + received)
		initiated	received	terminated	
I		1145	136	999	1281
% of row		89.4	10.6	77.9	
II		1302	156	1147	1458
% of row		89.3	10.7	78.7	
III		330	69	291	399
% of row		82.7	17.3	72.9	
Total		2777	361	2437	3138
% of Total		88.5	11.5	77.6	

Figure 1 Percentages of the Frequency of Interactions
within Age Classes

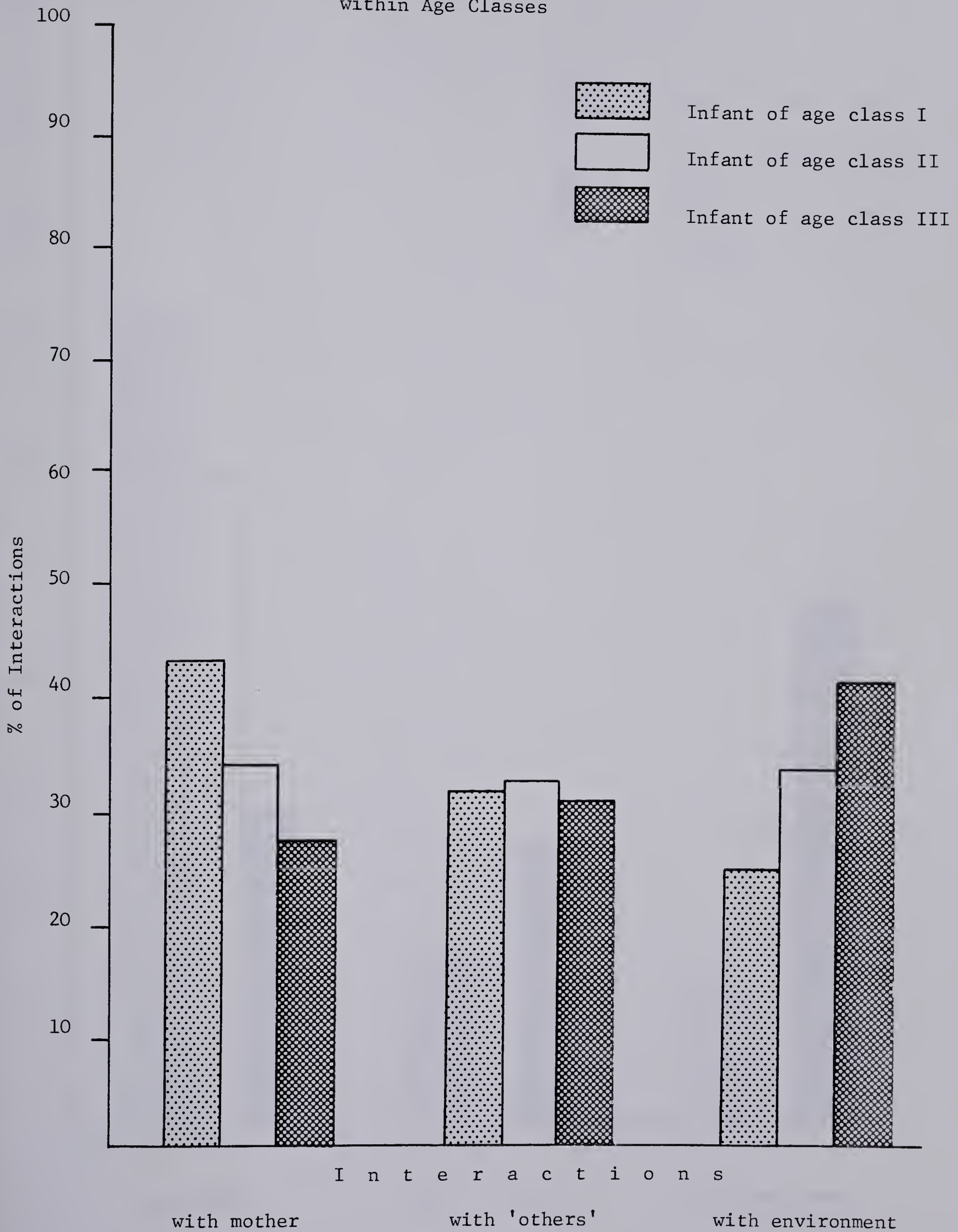


Figure 2

Percentages of the Duration of Interactions

within Age Classes

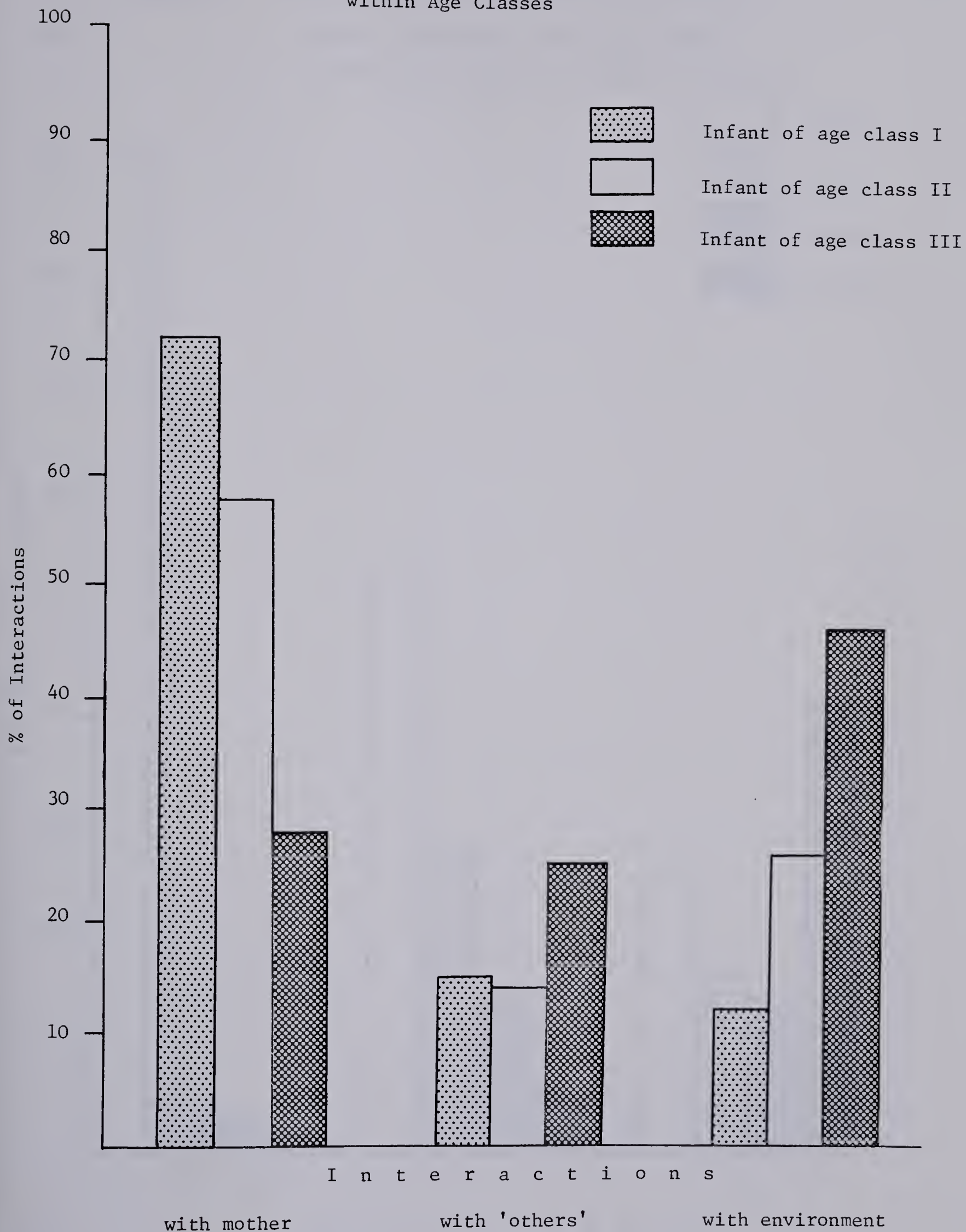


Figure 3 Frequencies of Social Interactions between a
Howler Infant and other Group Members
(accumulated frequencies from all 6 groups)

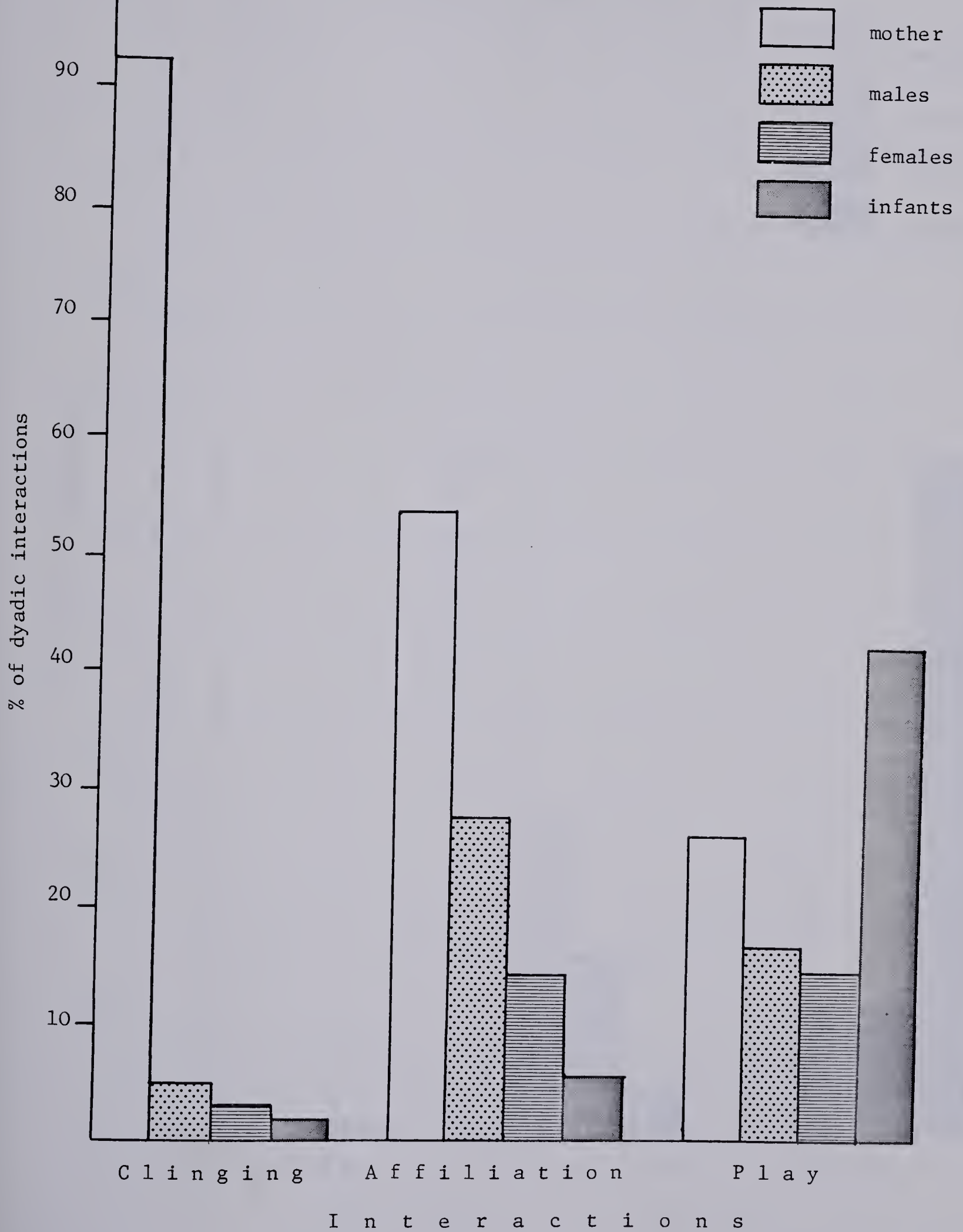
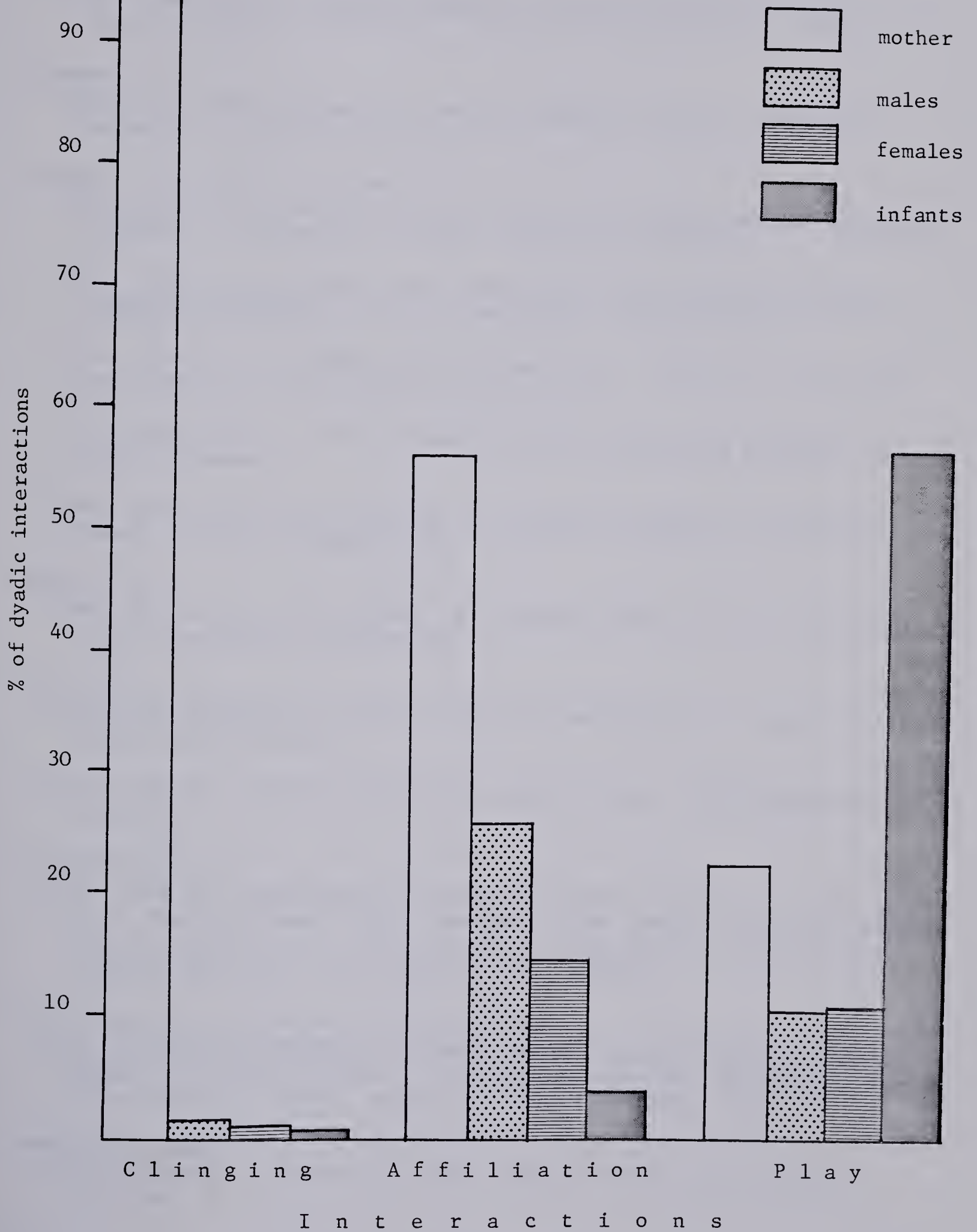


Figure 4

Duration of Social Interactions between a
Howler Infant and other Group Members
(accumulated values from all 6 groups)



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APPENDIX ONE

DATA SHEET

Subject: MI₃ group IV Date: Jan. 22 Time: 15:35

Context: Mo, AM and MJ₂ in close vicinity of MI₃

Time	Initiator	Receiver	Activity	Comments
15:35	<u>Mo</u>	I	muz	
15:36.4	<u>Mo</u>	I	tou	Mo pulls I's head toward hers tou head with both hands.
15:37.1	<u>I</u>	Mo	tou	I touches Mo's head with one hand.
15:38	I	AM	sit	
15:38.6	<u>AM</u>	I	hug	AM puts arm around I, pulls it toward him.
15:39.6	I		loc	2 meters from AM
15:41	<u>I</u>	AM	Cli	climbs across back
15:41.4	I		plo	Pulls branchlet toward body then lets snap out

underlined animal terminates interaction

APPENDIX TWO

ETHOGRAM

1. CVR: Infant is clinging ventrally while support animal is resting or sleeping. Neither of the animals involved in this interaction are moving; the infant may or may not be nursing.
2. CDR: Infant is clinging dorsally while support animal is resting or sleeping.
3. CVM: Infant is clinging ventrally while support animal is moving. The support animal may be foraging or locomoting to a different feeding or resting area.
4. CDM: Infant is clinging dorsally while support animal is moving. The support animal may be foraging or locomoting.
5. SIT: Sitting in close body contact. The animals may have their eyes open or closed.
6. SIV: Sitting in the vegetation. During explorations of the larger environment an infant may sit for any length of time in one spot while resting or manipulating leaves.
7. LOC: Refers to movement from one location to another. Does not include playchases or arboreal gymnastics. Locomoting can be fast or slow.
8. FOL: Following..An infant follows a group member in close body contact or vice versa, sometimes holding onto the tail or fur of the other animal.
9. FEE: Feeding or nibbling on leaves. It was not always clear whether an infant was actually ingesting leaves or just investigating them with its mouth.
10. GRO: This refers to grooming.
11. HUG: Hugging. In this behavior either one animal does the hugging while the other is being hugged, or both animals put their arms around one another while hugging.
12. HUD: Huddling. The animals involved in this behavior lean closely against one another, intermittently moving their legs rubbing their bodies together.
13. MUZ: Muzzling. Two animals touch one another with their noses or rub noses.
14. TOU: Touching. A friendly gesture where one animal touches a part of another animal's body with one or both hands.

15. PLA: Playing. This refers to play activities where both animals actively participate. This generally refers to rough-and-tumble play among infants or to a more gentle type of play between an infant and a group member other than a peer.
16. PLB: Play with part of another animal's body. For example, infants are often seen to play with the fur, ears or tail of a group member.
17. PLO: Play with an object. This refers to exploratory play where an infant manipulates leaves and branchlets.
18. CLI: Climbing over a group member. This is mostly done with a playful bouncy gait. Infants often repeat this several times in a row.
19. PLG: Play - arboreal gymnastics. The infant is swinging by its tail or limbs, intermittently jumping into the vegetation.
20. AGG: Aggression. Refers to one animal hitting, slapping or roughly pushing another.

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